

EMBRYOS AND ANCESTORS

BY

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PREFACE

TEN years ago I published a book under the title *Embryology and Evolution*, in which I made an attempt to show that after rejecting the theory of recapitulation, a much better synthesis could be made of our knowledge of embryonic development and evolutionary descent, opening up new fields for observation and co-ordination of studies in embryology, genetics, and evolution. This work has for some little time been out of print, and I have yielded to the demands of my friends to produce it again.

During the intervening years a great deal of new evidence has become available, and these fresh data have fitted into place in my scheme like pieces of a puzzle, for I have seen no reason to alter the plan of my former book in the slightest degree. The present book is my previous one brought up to date and enlarged.

I have recently been engaged in a study of the bearings of embryology on homology, taxonomy, and other special aspects of zoology. My views on these matters have been published in *Evolution: Essays presented to Professor E. S. Goodrich*, edited by myself, and in *The New Systematics*, edited by J. S. Huxley. I have therefore not felt called upon to repeat them here, except in so far as they bear directly on the problem of the relations between embryology and evolution.

It has been very encouraging to me to note the lively interest in these problems shown in recent years. The first necessity in Biology will always be further observation and experiment; but as Dr. Woodger aptly points out, progress in thought is necessary as well. Outworn theories are not only dull in themselves, but they are actually harmful in thwarting the framing of new working hypotheses which take account of recent progress made in the various experimental branches of Biology. Such an outworn theory I believe Haeckel's theory of recapitulation to be.

I lay no claims to proficiency in metaphysics, and I have no doubt that many of my expressions will appear sinful to my philosophical friends. But I am aware of many of the dangers, and when I say that 'paedomorphosis does this, that, or the other'

I am merely saving time and space, and not endowing an abstract concept with the powers of a subject of a transitive verb.

I should like to acknowledge my debt to M. Jean Rostand who translated my previous book into French. Few exercises are as helpful for testing the soundness of one's deductions and conclusions as the expression of them in another language.

I wish likewise to record my indebtedness to Dr. J. S. Huxley, Professor W. Garstang, and Professor J. B. S. Haldane for their helpful criticism, and to Professor R. A. Fisher for very kindly reading the proofs.

April 1940.

G. R. DE B.

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I

STAGES OF DEVELOPMENT AND STAGES OF EVOLUTION

EMBRYOS undergo development; ancestors have undergone evolution, but in their day they also were the products of development. Our first task must therefore be to define these two sets of events to which living things are subject. We shall confine ourselves to animals in this study, but what we shall have to say about them is, in general, applicable also to plants.

The life of an animal may be said to start from the egg which has just been fertilized. The egg is a more or less spherical object and it bears no resemblance to the animal that laid it, or into which it will develop. The processes of development are therefore concerned with the transformation of the egg into that form which we recognize as 'the animal'. The transformation is gradual, and so the shape of the spherical egg is modified little by little into another shape, and this is changed into yet different ones which succeed one another until the definitive or adult shape is reached. During its development, therefore, the animal passes through a series of successive stages, and it is the sequence of these stages which we mean when we speak of the animal's *ontogeny*. Some of the ontogenetic stages are familiar to every one, such, for example, as the caterpillar of the moth or the tadpole of the frog. But, on the whole, the stages of development of animals are more or less unknown to the layman, and he must rely on the embryologist, whose business it is to collect and study these interesting phases of an animal's existence.

Another series of stages can be made out from animals by comparing the full-grown or adult shapes of one kind of animal with those of other kinds, and finding that they can be arranged in an order of increasing or decreasing complexity. Such an order was not unknown to the Greeks, who called it the *scale of beings*. At the top of Aristotle's scale was man, below whom came whales, viviparous quadrupeds (other mammals), oviparous quadrupeds (reptiles and amphibians) and birds, and, below these, a medley of animals which Aristotle regarded as

being without blood, and in which we can recognize what we call the invertebrates, consisting of octopus, lobsters, insects, snails, starfish, and sponges, in descending order. A couple of thousand years later, the scale of beings received complete expression at the hands of Bonnet, who strung out all the animals, plants, and minerals which he knew on a long ladder, of which they formed the rungs.

It was natural that the thought should arise of comparing the two series which we have now just seen—the sequence of ontogenetic stages and the successive shapes of animals on the scale of beings. This idea seems to have occurred to Harvey, for, when speaking of development, he says: 'Nature, by steps which are the same in the formation of any animal whatsoever, goes through the forms of all animals, as I might say egg, worm, embryo, and gradually acquires perfection with each step.' The same notion is expressed in the following passage of John Hunter: 'if we were capable of following the progress of increase of the number of the parts of the most perfect animal, as they first formed in succession, from the very first to its state of full perfection, we should probably be able to compare it with some one of the incomplete animals themselves, of every order of animals in the Creation, being at no stage different from some of the inferior orders.' So also Serres: 'Man only becomes man after traversing transitional organizatory states which assimilate him first to fish, then to reptiles, then to birds and mammals.' Similar ideas were also expressed by Meckel.

According to these views, therefore, the ontogenetic series and the scale of beings run parallel with one another, and the developmental stages of an animal are held to correspond to the definitive or adult stages of animals lower down on the scale.

While the scale of beings was gradually being amended and expanded as new animals came to the notice of naturalists, the foundations of an accurate descriptive knowledge of the ontogenetic stages through which animals pass in their development were not laid until the work of von Baer. As a result of his extensive researches, von Baer came to a number of conclusions which are expressed in the form of four statements; these have come to be known as the 'laws of von Baer'. As they are of the greatest importance from the present point of view, they are here repeated:

1. In development from the egg the general characters appear before the special characters.
2. From the more general characters the less general and finally the special characters are developed.
3. During its development an animal departs more and more from the form of other animals.
4. The young stages in the development of an animal are not like the adult stages of other animals lower down on the scale, but are like the young stages of those animals.

By his 1st and 2nd laws, von Baer expressed the fact that in the development of the chick, for instance, there is a stage at which he could recognize it as a vertebrate but could not say what kind of vertebrate it was; and that at a later stage when he could recognize it as a bird it was still impossible to distinguish which kind of bird. The 3rd and 4th laws express von Baer's most important contribution, which is that animals are more similar at early stages of their development from the egg than when they are full-grown, and that this resemblance between early stages becomes progressively diminished as they grow older. Indeed, of a couple of embryos which von Baer had preserved in spirit, he was unable to say whether they were reptiles, birds, or mammals, so similar are the young stages of these animals. Instead, therefore, of passing through the adult stages of other animals during its ontogeny, a developing animal moves away from them, according to von Baer, and the ontogenetic stages do not run parallel to the sequence of forms of the scale of beings.

The introduction of the concept of evolution was obviously destined to make important changes in the consideration of the relations of ontogeny to the scale of beings. For the scale of beings then ceased to be a mere static row of shapes of adult animals, and, instead, became a line of ancestors which by modification in descent have evolved into other (and usually more complex) forms. The modifications undergone by the shape of the adult animals in successive generations during evolution could now be regarded as a series of stages in the history of the race, which series became known as the *phylogeny*. The problem now was to see how ontogeny and phylogeny were related, and the next step in this direction was taken by Fritz Müller. For Müller, ontogeny could follow one of two

methods. During its development from the egg, an animal might either pass through the ontogenetic stages and beyond the final adult stage of the ancestor ('overstepping'), or it might diverge more and more from the ontogenetic stages of the ancestor (progressive deviation). The former mode reflects the theory of parallelism of Harvey and Serres, the latter gives expression to von Baer's theory of the greater resemblance between animals when they are young. It is important to notice that Müller bases phylogeny on ontogeny, for it is the changes in ontogeny (i.e. alteration in the processes of development of the descendants as compared with those of the ancestor) which make the adult descendants differ from their ancestors, and so add a new link to the phylogenetic chain.

This was the state of affairs when Haeckel took the matter up and expressed his views of the relation of ontogeny to phylogeny in the form of his famous theory of *recapitulation* or *biogenetic law*. According to this, ontogeny is to be regarded as a short recapitulation of phylogeny, and *phylogeny is the mechanical cause of ontogeny*. The adult stages of the ancestors are repeated during the development of the descendants, but they are crowded back into earlier stages of ontogeny, therefore making the latter an abbreviated repetition of phylogeny. These repeated or 'recapitulated' stages reflect the history of the race, and so Haeckel applied to them the term *palingenetic*. As an example may be mentioned the stage in the unhatched bird and unborn mammal when gill-slits or pouches are present. Haeckel urged that these gill-slits represented gill-slits of the adult stage of the ancestral fish, which in the birds and mammal has been pressed back into early stages of development.

At the same time, it could not be denied that in some cases, at least, the young stages of a developing animal presented shapes and structures which no adult ancestor could possibly have possessed, such as the birth-membranes of a mammal for instance. In these cases, Haeckel concluded that the recapitulation of palingenetic stages was temporarily in abeyance and that a new or *caenogenetic* stage had been intercalated in the ontogeny as an adaptation to some inevitable conditions which the mode of life of the young animal imposed. The caenogenetic stages, therefore, had no ancestral or historic significance.

It will be noticed that the biogenetic law abandons von

Baer's principle of progressive deviation, or rather relegates it to the state of the caenogenetic exceptions, and that it is really a reversion to the theory of parallelism and the 'overstepping' of Müller, to which it adds the causational idea that the succession of palingenetic stages in ontogeny is due to these stages having succeeded one another in phylogeny. The biogenetic law makes it necessary to believe that the new variations (by means of which evolution was brought about) occurred at the end of the ontogeny of the ancestor, or in other words, that the evolutionary novelty first appears in the adult. Phylogeny, then, according to Haeckel, is brought about by the successive tacking of new final stages on to the existing adult stages of animals, and the processes of development in ontogeny are 'due' to this progressive accumulation in phylogeny. What 'due' may mean we shall see in the next chapter.

Seeming confirmation of Haeckel's views was provided by the work of Hyatt and Würtemberger on ammonites. These fossil animals had shells which were constantly added to during their life. The above-named authors thought that they could show that the characters which appeared on the older parts of the shell of an ancestral ammonite were to be found on the younger parts of the shell of subsequent and descendant ammonites. At all events, this view commended itself to Weismann, who summed up his opinion as follows: 'The ontogeny arises from the phylogeny by a condensation of its stages', which he also expressed as 'a retraction of the phyletic (phylogenetic) acquisitions of the mature animal deeper and deeper into the germinal history of the species'.

The theory of recapitulation has been provided with an elaborate terminology. 'Tachygenesis' is the speeding-up and compression of ancestral stages in developments, 'lipogenesis' is the omission of certain stages, 'bradygenesis' the lengthening of certain stages.

At the present day the theory of recapitulation still has its supporters. From the embryological point of view, MacBride states that 'the larval (i.e. early) phase of development represents a former condition of the adults of the stock to which it belongs'. Further, when comparing the young stage with 'the adult ancestral stage which it represents . . . one receives the impression that one is dealing with a reaction which, constantly

repeated through thousands, nay myriads of generations, tends to set in sooner and sooner in the course of development; just as in the life of the individual, the *formation of habit* causes reactions to require for their evocation less and less of the original stimulus'. From another point of view, Smith Woodward, speaking as a palaeontologist, says that he is 'convinced that whenever he is able to trace lineages he finds evidence of the recapitulation of ancestral characters in each life-history', and 'he is equally convinced that the phenomena he observes when tracing lineages can only be explained by assuming that acquired characters are inherited'. These two authors thus propose to relate phylogeny to ontogeny by means of the inheritance of acquired characters. Quite apart from whether we accept or reject the inheritance of acquired characters (and we shall have something to say about this in the next chapter), it must be borne in mind that the relation between ontogeny and phylogeny is to be looked for and found in heredity.

Such is the history of the development of thought which has led to the theory of recapitulation. This still has a remarkable sway. It is responsible for the fact that so many biological examination papers answered by schoolboys contain the statement that 'during its life-history an animal climbs up its family tree'. The criticism to which the biogenetic law and theory of recapitulation have been subjected seems to have made but little impression, for the schoolboys' answers do not change, and yet these criticisms have not been unimportant. In the first place it was pointed out (by Agassiz, Keibel, and Mehnert among others) that the order in which characters appeared in phylogeny is not always faithfully reproduced in ontogeny. For instance, teeth were evolved before tongues, but in mammals now tongues develop before teeth. To this alteration and reversal of the sequence of stages the term *heterochrony* is applied, and it creates the suspicion that the alleged retraction of adult characters into younger stages of development (if it really occurs) is not simply due to the piling up of new variations at the end of the life-history, for the order of the pile is not necessarily respected. It also suggests that it is not legitimate to speak of a 'stage' being shifted back to a later or on to an earlier period in the life-history. It is not the 'stage' which is shifted *en bloc*, but certain characters which may be peculiar to the stage. It

must also be remembered that what an embryologist calls a 'stage' is merely an arbitrarily cut section through the time-axis of the life of an organism. A 'stage' is thus really an abstraction of the four dimensional space-time phenomenon which a living organism is.

Another line of attack was made possible by the increase in detailed knowledge of the young stages. Sedgwick showed that the earlier stages of development of quite closely related animals (such as the hen and the duck) could be distinguished, and W. His concluded that, even at these early stages, developing animals possess the characters of the class, order, species, and sex to which they belong, as well as individual characteristics. O. Hertwig went on to point out that the very egg itself must have specific characters although they may be invisible, and that the eggs of two different animals are really as distinct from one another as are their adults, the distinctions becoming more and more visible as development proceeds. The egg of the mammal and the unicellular ancestor are not really comparable, and in a remarkably thorough analysis Hertwig revealed this flaw in the logic of Haeckel's argument. In the same vein, T. H. Huxley concluded that 'there is no real parallel between the successive forms assumed in the development of the life of the individual at present, and those which have appeared at different epochs in the past'. F. R. Lillie also has pointed out that not only the final result but all the stages of ontogeny are modified in evolution.

Recently, Garstang has elaborated this view very skilfully, and has shown that there has been an evolution along the line of fertilized eggs (or zygotes), in consequence of which animals have modified their ontogenies and so changed the shape of the final stage of development, viz. the adult. But a series of adult forms modified in this way is phylogeny, and so phylogeny is the result of ontogeny instead of being its cause. Garstang has thus arrived at the same point of view as Hurst, who wrote: 'I do deny that the phylogeny can so control the ontogeny as to make the latter a record of the former.' An identical point of view has since been expressed by Ekman, Franz, Fuchs, Nauck, Schindewolf, and Shumway. Similarly, Berg allows that ontogeny anticipates phylogeny.

Among other recent critics may be mentioned Naef, who by

his 'law of terminal alteration' redirects attention to von Baer's principle of greater resemblance between young stages; Sewertzow, whose principle of 'anaboly' resembles the 'overstepping' of Müller, and whose 'archallaxis' savours of the principle of deviation; Franz, who proposes four methods ('biometabolic

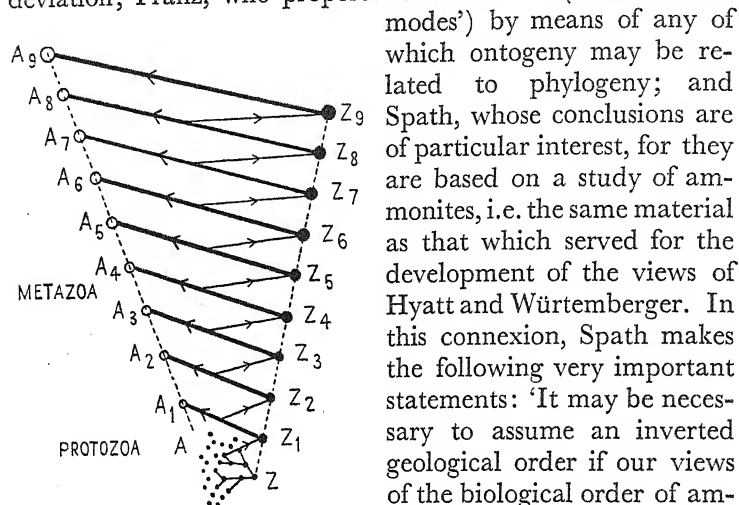


FIG. 1. The relations between ontogeny and phylogeny. Z_1-Z_9 , the succession of zygotes; A_1-A_9 , the succession of adults (phylogeny); Z_1-A_1 , Z_2-A_2 , the succession of ontogenies. From W. Garstang, *J. Linn. Soc. Lond. Zool.* 35, 1922.

of the views on ammonite development connected with the names of Hyatt and Würtemberger.'

Furthermore, as a result of detailed studies on Jurassic ammonites, Brinkmann has been led to the conclusion that the so-called biogenetic law is by no means of universal application. While in some lines, ontogeny appears to run parallel with phylogeny, in others, this is not the case. Here, 'phylogeny has lost its influence over ontogeny'.

George, a defender of the biogenetic law, is forced to admit that 'the application of the law must be tentative rather than final; it is approximate, rather than exact; it suggests and implies rather than fulfils'.

modes') by means of any of which ontogeny may be related to phylogeny; and Spath, whose conclusions are of particular interest, for they are based on a study of ammonites, i.e. the same material as that which served for the development of the views of Hyatt and Würtemberger. In this connexion, Spath makes the following very important statements: 'It may be necessary to assume an inverted geological order if our views of the biological order of ammonites are to continue to be governed by discredited "laws" of recapitulation'; and 'when the horizons of all these stocks are definitely known, it is hoped to get good additional evidence for a final rejection

Swinnerton in a careful and critical study recognizes that not only ancestral adult but also young characters can be recapitulated, or, as we prefer to say, repeated. And he makes clear that the repetition of a character is far from being the reconstitution of an ancestral stage.

Kryžanowsky, the most recent author to consider the theory of recapitulation, has subjected it to a devastating analysis. He knows of 'no single case in which evolutionary modification of ontogeny has taken the form of addition of new terminal phases to the final phases of the old ontogenies'. He objects on logical grounds to a comparison between ontogeny on the one hand, and the final stages of ontogeny on the other. Phylogeny he, like Garstang and Swinnerton, regards as the succession of *complete* ontogenies, and since *all* evolutionary ontogenetic novelties are repeated in some phase or other of subsequent ontogenies (i.e. have 'phylogenetic' significance), Haeckel's distinction between palingenetic and caenogenetic characters falls to the ground.

It is obvious, then, that with regard to the relation which may exist between ontogeny and phylogeny, there is a basic divergence of opinion. While some continue to place phylogeny as a cause acting in and behind ontogeny, others prefer to reverse this relation. The matter is important, for it concerns the kernel of biology—development, evolution, and heredity. And, far from the question being one of merely academic interest, it is of the greatest practical importance, for the prestige so long enjoyed by the theory of recapitulation has had a great and, while it lasted, regrettable influence on the progress of embryology. This will be shown in due course. The following pages are therefore devoted to an attempt to synthesize the existing state of knowledge in these three fields and to produce a consistent formula which will co-ordinate them all.

For that which Sedgwick wrote 30 years ago is true to-day: 'if after 50 years of research and close examination of the facts the recapitulation theory is still without satisfactory proof, it seems desirable to take a wider sweep and to inquire whether the facts of embryology cannot be included in a larger category.'

II ONTOGENY

IN the development of any organism, we have to distinguish between the internal factors which are at work inside it and the external factors which constitute its environment. Now the internal factors were present in the fertilized egg, and so they can also be regarded as the transmitted factors, passage of which from parent to offspring constitutes heredity. When, therefore, we ask the question: Do the internal factors which are present in the fertilized egg suffice to account for the normal development of an animal? we are also questioning in how far heredity is responsible for the sequence of processes which constitute ontogeny. And since phylogeny can only be related to ontogeny through heredity, we are testing the validity of Haeckel's statement that phylogeny is the mechanical cause of ontogeny. Fortunately, our knowledge of the processes of development has recently been very greatly increased by the extension of the application of experimental methods to the study of embryology. It may be definitely stated that the internal factors which were inherited from the parents are *not* sufficient to account for the development of an animal. To illustrate this all-important point, we may refer to the fact that ever since the Silurian geological period, roughly 300 million years ago, vertebrate animals had two eyes, as can be proved from a study of the fossils. Since, then as now, there must be internal factors concerned with the production of the two eyes, these have been transmitted to every generation for a very considerable period. But these factors are not self-sufficient, for if a few pinches of a simple salt (magnesium chloride) are added to the water in which a fish (*Fundulus*) is developing, that fish will undergo a modified process of development and have not two eyes, but one, as Stockard showed. Countless similar examples might be given, but this one suffices to show that by themselves the internal and therefore transmitted factors are not able to 'produce' a normal animal.

Numerous experiments have shown that the internal factors of an animal are possessed equally by the cells in all its parts.

So the cells of the head of a worm can by regeneration produce a tail, and the cells of the tail can regenerate a head. But if the cells of the head possess the internal factors which control the production of a tail as well as the internal factors which control the production of a head, how is it that in normal development these cells do produce a head and not a tail? Child has solved this problem by showing experimentally that the first thing which has to be settled in a developing egg is the polarity, i.e. which part of the egg will give rise to the front and which to the hind end of the future animal. As soon as the polarity is established, local diversities arise and result in the qualitative differentiation of the different parts. Now in many cases, the determination of this polarity seems to be the result of the action of factors which are *external* to the fertilized egg. In other cases it is possible that the polarity of the egg is derived from that of the oogonium which gave rise to it, but this merely pushes the question of the origin of polarity back in time. However this may be, it is clear that all the way through development the internal factors produce nothing of themselves, but they enable the animal to react in definite ways to the external factors and by this means give rise to structure after structure in the process of development. Heredity does not account for the individual, but merely for the potentialities some of which are realized in the individual. In other words, the internal and transmitted factors are by themselves unable to 'produce' an animal at all.

The first rigorous analysis of the relation of internal and external factors in development is due to Lankester, who showed that they can only be regarded as co-operating in the production of all the characters of an organism. The same point of view has been developed by Goodrich, who stresses the distinction which has to be drawn between the process of transmission of the internal factors from parent to offspring, and the process of production in the offspring of characters similar to those which were possessed by the parent. 'An organism is moulded as the result of the interaction between the conditions or stimuli which make up its environment and the factors of inheritance. No single part is completely acquired, or due to inheritance alone. Characters are due to responses, and have to be made anew at every generation.' Similar views have been

expressed by Conklin. These conclusions, which are based on definite experimental evidence, have a far-reaching importance. In the first place they show that the question—Are acquired characters inherited?—has no meaning, and that what the questioners really mean is—Can an effect originally produced as a response to an environmental stimulus come subsequently to be produced regularly without that stimulus? In other words, can external factors become internal? When, therefore, Hyatt defined an acquired character as 'a modification which makes its appearance in the adult or later stages of development and is obviously dependent for its origin upon other than hereditary causes', he is really describing the effect of an external factor, but that does not justify him in excluding the participation of internal factors in producing that effect.

We shall return below to the question whether external factors may become internal, and may go on now to note that the conclusions at which Child and Goodrich have arrived lift a great burden off the problem of heredity. The structure of an animal shows a number of exquisitely delicate adjustments; the splinters inside a bone are situated exactly where they are required to withstand the pressure to which the bone is subjected; the fibres of a tendon lie accurately along the line of strain between a muscle and the bone to which it is attached; centres of nerve-cells in the brain are situated close to the ends of the nerve-fibres from which they habitually receive impulses, and when in phylogeny there is a change in the nerve-fibres from which any given nerve-centre habitually receives its impulses, the nerve-centre is found to be situated near its new source of stimulation. It is this appearance of change in the position of nerve-centres during evolution which Kappers has designated under the term *neurobiotaxis*.

It was a source of much perplexity to the student of heredity to try to understand how the factors controlling the production of such intricate and refined adjustments could be transmitted to the fertilized egg and produce these effects. He need not have worried about the production of the effects, for that lay in the province of the experimental embryologist, and not in his. As it turns out, it is the pressure in the tissues which causes the cells along the lines of stress to produce splinters of bone, and that is why these splinters are in the 'right' place; it is the

very pull exerted on the tissues by the muscles which determines the production of a tendon with its fibres orientated along the lines of strain; it is the very ends of the nerve-fibres which have the property of stimulating nerve-cells to divide and so produce a nerve-centre in proximity to them, as Detwiler has proved. The nerve-centres arise afresh in each generation, and by arising in a different place under the stimulation of a different set of nerve-fibres, the apparent effect of a migration in phylogeny receives its explanation.

All that is required is the transmission by internal factors of the capacity to react in these ways to new stimuli which evoke one response after another.

It is obvious on looking back over the subject-matter of this chapter that ontogeny cannot be regarded simply as an extrapolation into the future of a chain of events which happened in past and previous generations. Each ontogeny is a fresh creation to which the past contributes only the internal factors by the means of heredity. And this past is not the phylogenetic line of ancestral adults, but the line of the germ plasm supplying the fertilized eggs for each and every generation. The action of the internal factors is to ensure that if the external factors are normal and do evoke any response in development and produce an animal at all, that animal will develop along the same lines as its parent. The internal factors are only a partial cause of ontogeny.

We may now turn to the question whether the internal factors which are operative in ontogeny can in any way be regarded as the result of the modifications which the ancestors underwent in evolution resulting in phylogeny; or, in other words, whether phylogeny is in any way a 'cause' of ontogeny. If these modifications which the ancestors underwent were the result of changes in the internal factors, then the question can be answered at once, or rather it does not arise, for in this case the phylogeny will itself have been the product of the internal factors working in ontogeny. But if, on the other hand, the modifications which the ancestors underwent in phylogeny were due to changes in the external factors, then these external factors could only become the cause of the internal factors which control that same modification in subsequent ontogenies in so far as they can be converted from external into internal

factors (i.e. in old terminology, in so far as 'acquired' characters can become 'inherited').

Now the recent work of Muller and others has shown that it is possible to produce a permanent change in the internal factors as a result of stimulating the animal with special external factors, but these external factors did not produce any modification in development at all before they became internal. Exposure of flies to X-rays does not affect their bodies, although it can 'produce' an internal factor which will ensure that later ontogenies will result in animals modified in a particular way. These experiments have shown the possibility of 'direct induction' of a change in the internal factors by external factors. They have not shown the possibility of 'somatic induction', i.e. of a change in the internal factors produced by an adaptive change in the structure of the body, which latter change was itself produced by external factors. To put the matter as clearly as possible, it seems that no case has yet been satisfactorily proved in which the development of an ancestral animal has undergone a modification as a result of external factors and in which these external factors have become internal and transmitted, so that the same modification has come to be invariably produced in all the subsequent ontogenies of descendant animals in the absence of these external factors which originally evoked the modification. Until such a case has been proved it cannot be believed that the effects of use and disuse on body or mind are transmitted, and it cannot be stated that phylogeny plays any part in ontogeny at all, even in the restricted part played by the internal and transmitted factors.

Somatic induction, or the transmission of the effects of use and disuse, constitute the kernel of the Lamarckian point of view; and it is curious that while we still want evidence of this, Lamarck ruled out that of which we have evidence, viz. direct induction, though of course he was correct in rejecting the view that direct induction can produce an adaptive inherited response to the environmental stimulus.

III

THE SPEEDS OF THE PROCESSES OF DEVELOPMENT

WE have seen in the previous chapter that development was brought about by means of the interaction of internal and external factors. Granted that the external factors remain constant and normal, we have now to inquire into the way in which the internal factors produce their effects. These internal factors have recently been subjected to very intense study, but only as regards the mechanism of their transmission from parent to offspring. They are now called Mendelian factors or genes, and are regarded as discrete units situated in or on those universal constituents of the nuclei of cells—the chromosomes. A change induced in one of these genes is called a mutation, and the gene is then fixed in this changed condition until it mutates again. It is now usual to regard these mutations, and recombinations of genes at the fertilization of eggs by sperms, as responsible for the appearance of novelties in evolution.

The way in which the genes are sorted out and distributed between parent and offspring is well known as a result of Morgan's continuation of Mendel's lead, and forms the subject-matter of the science of genetics. In the process of their transmission the genes are carried in the germ-cells, the egg, and the sperm. Germ-cells, like all cells, only arise by the division of pre-existing cells, and the production of ripe germ-cells occupies two cell-generations. It is during these two cell-generations (which culminate in fertilization) that the distribution of genes takes place, and so the geneticist who studies this distribution in hereditary transmission is really following the genes through two cell-generations only. But it takes fifty-six generations of cells to produce a body like that of a man out of a fertilized egg (itself a single cell), and during these fifty-six generations the genes are playing their part in company with the external factors in moulding the animal through the successive stages of ontogeny. We now want to know how this part is played.

This question is only beginning to be asked, and the lines on which it is to be answered have been indicated by

Goldschmidt. In his work on the determination of sex in the gipsy moth, he has shown that the structure of the adult, according to whether it is male or female, depends on the relative speeds at which two sets of genes produce their effects. These two sets may be referred to as the male-producing and the female-producing genes. In other words, genes as factors do not only have qualitative values; each gene also has a specific quantitative value and reaction-rate. Various races of the gipsy moth have male-producing (and female-producing) genes of different quantitative value. By introducing into an egg containing a weak female-producing gene a sperm containing a strong male-producing gene (as may be done by crossing moths of different races), it is possible to convert would-be females into males more or less completely. The conversion takes place at a certain time in development when the stronger male-producing gene overtakes its rival (the female-producing gene). Up to this point the female-producing gene has been ahead and the animal has been developing along female lines, but from the point of conversion onwards, the male-producing gene is leading and the animal then finishes its development along male lines. The stronger these male-producing genes, the sooner do they overtake their rivals, the earlier the time of conversion from one type of development to the other, and the more complete will be the conversion from female to male. Such animals which have switched over from a period of development in one sex to a period of development in the other are called intersexes, and a series of degrees of intersexuality can be established, from very slight to complete sex-reversal. In this series it can be noticed that the various organs and parts of the body do not all switch over from maleness to femaleness together, but one after another in a definite order, along a scale of increasing intersexuality. An organ which has finished its development before the time of conversion remains wholly female. Since the conversion takes place only after a definite point in time, the organs which are affected in cases of a slight degree of intersexuality should, on the theory, arise late towards the end of ontogeny, while those organs which arose earlier, i.e. before the time of conversion, will not be affected. In order to get at these latter organs and to switch them over from femaleness to maleness, it is necessary to have the overtaking

of the female-producing genes by the male-producing genes happening sooner, which will be the case if the latter are very strong. The theory, therefore, rests on the assumption that the various organs develop in a certain definite order in time. Now this assumption can be tested independently of the evidence on which the theory is based (which was the varying degrees of intersexuality), by simply studying the development of the gipsy moth. When this was done it was found that the order of development of organs is precisely that which the theory demanded. There is therefore a definite experimental basis for the statement that genes can control the structure of the body and can alter that structure by varying the rate at which they work.

An analogous case was investigated by E. B. Ford and J. S. Huxley in the brackish water-shrimp *Gammarus*. Some of these animals have black eyes and some red, and whether they have eyes of one or the other colour is determined by genes. These genes produce their different effects by varying the speed at which they allow the deposition of black colouring matter covering the red, and the time of onset of the processes.

Another example is that of the colour of the caterpillars of the gipsy moth, studied by Goldschmidt. The pattern on the back of the caterpillars in some races becomes obscured by black pigment, and the rapidity of the deposition of this pigment is under the control of genes. Similarly, the time of onset of the deposition of pink pigment on the shell of the snail *Cepaea* is controlled by genes, as Diver has shown. Genes likewise control the rate of formation of the pigment cells in the skin of goldfish, as H. B. Goodrich and I. B. Hansen have found.

The difference in size between large and small rabbits is due to different rates of cell division, which rates, as Castle and Gregory have shown, are under the control of genes. Differences of shape are the result of different rates of growth in different directions, and these have been shown in gourds and peppercorns to be controlled by genes. Details of these and other cases are given by Sinnott and Dunn.

That the general idea is true that the genes produce their different effects by working at definite speeds can further be shown by raising or lowering the temperature of the environment, which accelerates or retards the rate of action. This is why a primrose which at a temperature of 20° C. has red flowers,

will have white flowers if it is grown at 30° C. It also supplies the reason why the fur of the extremities (ears, paws, and the tip of the tail) of Siamese cats is dark, for the temperatures at these places is lower than in the body generally.

We therefore reach the conclusion that by acting at different rates, the genes can alter the time at which certain structures appear, viz. in the case described, male structures in would-be female gipsy moths, and black eyes in *Gammarus*. This conclusion is of considerable interest, for it enables us to see how heterochrony can take place. It may be imagined that a character *A* was evolved in phylogeny before a character *B*, but there is no reason why in ontogeny character *B* should not arise before, simultaneously with, or after, character *A*, according to the relative speeds of the genes at work, and the environmental conditions. A character which appeared in the adult stage of the ancestor might develop early in the ontogeny of the descendant, and vice versa. Kryžanowsky gives examples.

Haldane has devoted a study to the times in ontogeny at which genes exert their effects. He has shown that a gene may act: (1) on the germ-cells, (2) on the fertilized egg, (3) on the embryo, (4) on the larva, (5) on the developed but immature organism, (6) on the adult, (7) on the maternally-produced structures associated with the next generation (e.g. albumen, shell, placental decidua), (8) on the germ-cells of the next generation, (9) on the fertilized egg of the next generation. Haldane has provided examples of nearly all these possibilities from both the vegetable and animal kingdoms, and he has stressed the importance of the effects of heterochrony in changing the stages in ontogeny at which the genes may act.

Supposing that in a straight-shelled palaeozoic ammonite there was a gene of class (9) controlling the straight growth of the shell of the next generation, heterochrony might restrict the effects of the gene to the initial stages of development, the subsequent stages being characterized by curved growth. This is the condition of many mesozoic ammonites. Further heterochrony might convert the gene in question from class (9) to class (6) or (5). It would then exert its effect, not on the next generation, but on the final stages of ontogeny of the generation carrying the gene; the terminal whorls of the shell of such a form would be straight, as in many caenozoic ammonites.

Following up this line of thought, it may be asked what the effect would be if a gene of class (g) controlling rapid growth of the young stages of the next generation were to become accelerated so as to exert its effects in the later stages of its own generation. Presumably a tumour.

In the vertebrates, the development of several structures is under the control of chemical substances, the hormones, which are produced in special glands and circulate in the blood. In the frog, the thyroid hormone is of great interest, for it is concerned in the development of the limbs, the lungs, and the tongue, i.e. in the production of those structures which will turn the tadpole into the frog and so bring about the change which is called metamorphosis. If extra thyroid hormone is administered to a tadpole, it will metamorphose too soon; if its thyroid gland is removed it will not metamorphose at all, and the limbs, lungs, and tongue are not developed. The time at which metamorphosis normally occurs varies in different frogs and toads, and J. S. Huxley has shown that the differences in development of the following animals can be explained on the basis of the different rates at which the thyroid gland develops in each:

Bufo lentiginosus (toad) metamorphoses in early summer.

Rana temporaria (common frog) metamorphoses in late summer.

Rana clamitans metamorphoses in second season.

Rana catesbeyana (bull-frog) metamorphoses in third season.

The thyroid gland develops fastest in the first, which metamorphoses while it is still of small size, and slowest in the last, which reaches a much larger size before it metamorphoses.

Now there is little doubt that the speed at which the thyroid gland develops is itself under the control of genes, for Riddle, working on the thyroid of pigeons, came to the conclusion that the 'normal mechanism of heredity can operate in the perpetuation of small changes in the endocrine organs'. The differences between the toads and frogs just mentioned can therefore be indirectly referred to the different rates of action of the genes.

In mice, Smith and MacDowell have discovered a gene which controls the formation of the eosinophil cells of the pituitary gland. When these cells are absent, the mice are dwarfs, presumably because the cells produce the growth-

promoting substances. At all events, we have here definite evidence of the genetic control of endocrine function.

In the mammals the hormones acquire an increased importance in regulating the speed of development, and deficiency in the thyroid, for instance, is well known to be associated with the under-developed condition known as cretinism. When the balance of the different hormones is upset, the tempo of development may be seriously affected, as in the condition described by Gilford as progeria, in which a man became senile and extremely decrepit by the time he had lived only seventeen years. Compared with other mammals, the speed of development in man is very slow, as can be shown in the following comparison, which was made by Bolk:

Man takes 9 months to reach 3.5 kg. weight, and doubles it in 180 days.

Ox takes 9 months to reach 40 kg. weight, and doubles it in 47 days.

Some animals go on developing throughout their lives, but most cease altering their shape at a certain stage in ontogeny which is called the adult, and which is characterized by the fact that the reproductive organs are then ripe and ready to propagate the race. Now, the time at which the adult stage is reached is also governed by the rate of action of the genes, either directly, as in the gipsy moth, or indirectly by means of hormones, as in the case of the frogs and newts. It is possible, therefore, for there to be a competition between the genes which control any particular character and those which determine the assumption of the adult stage, and unless the former work fast enough and get in in time, the character will not be able to show itself. This is what actually happens in those cases in which an animal becomes sexually mature while still in the young stage, a phenomenon known as *neoteny* or *paedogenesis*. An example of this is furnished by the axolotl, which is really the tadpole stage of a newt (*Amblystoma*) and possesses gill-slits and external gills. In this state it can become sexually mature, and so some features of its structure, such as the bones of the skull, never become properly developed. Another example is the worm *Polystomum integerrimum*, which is parasitic on the frog, usually in its bladder, where it takes three years to reach maturity. But should it infect an early tadpole stage of the frog, it remains in the gill-chamber

and becomes sexually mature in five weeks. The structure of this neotenuous form differs from that of the normal worm in that it has but one male reproductive gland instead of several, and other structures such as the intromittent organ, vagina, and uterus are vestigial or absent. It is interesting to note that some animals have become permanently committed to this neotenuous state; so the newts *Proteus*, *Necturus*, and *Typhlomolge* resemble the axolotl, and *Polystomum ocellatum* resembles the neotenuous form of *Polystomum integerrimum*.

On the other hand, by delaying the time at which the adult state is normally reached, it is possible to cause structures to appear which would not ordinarily have done so. So in the case of the female gipsy moth, Goldschmidt was able to delay the onset of maturity sufficiently long for the male-producing genes to overtake the female-producing ones, and so bring about the formation of male structures in an otherwise normal female. It will be shown later that something like this has possibly taken place in the evolution of certain kinds of animals.

Altogether, then, we may safely conclude that the speeds at which the internal factors work are of great importance in development, and variations in the relative speeds of the various factors may play an important part in the relation of ontogeny to phylogeny.

IV PHYLOGENY

PHYLOGENY is the rehabilitated scale of beings, a row (or rather a number of rows) of adult forms which are related to one another, not from adult to adult, but from the fertilized egg which gives rise to one adult to the fertilized egg which produces the next. The adult forms in phylogeny are therefore disconnected, save for the (unproven) possibility mentioned at the end of Chapter II that the external factors which control the formation of an adult might become converted into internal factors, and so affect the ontogeny and production of the adult of the next generation.

It is pointed out by Garstang, Swinnerton, and Kryžanowsky that the restriction of the term phylogeny to the adults of the series is arbitrary, and that phylogeny should be regarded as the succession of complete ontogenies. This is true, and it must be noted that the upholders of the theory of recapitulation had adults in mind when they thought of phylogeny. But the cases in which the ontogenies of a phylogenetic series are known (ammonites, gastropods) are few. It is, therefore, more convenient to restrict phylogeny provisionally to mean the succession of adults. If all animals had been preserved as fossils, and if all these fossil remains had been discovered, we should be able to trace a continuous series of adult ancestral forms which would represent the phylogeny of the race which we were studying. Unfortunately this is not the case, for the fossil record is still imperfect, and we only have a number of more or less isolated forms to indicate the track which phylogeny has taken. Nevertheless, the study of the phylogenies of a number of animals such as the horse, elephant, and camel have yielded very interesting series showing the progressive modifications which these races have undergone during evolution. Now, on comparing the various members of a phylogenetic series, it appears that the differences between the structures of the adults are largely differences of proportion and of number of the parts relatively to one another. D'Arcy Thompson says in this connexion that 'it is certain that, in particular cases, the

evolution of a race has actually involved gradual increase or decrease in some one or more numerical factors, magnitude itself included—that is to say, increase or decrease in some one or more of the actual and relative velocities of growth'. In other words, phylogeny in these cases has been brought about by variations in the relative rates of action of the genes, which formed the subject of the last chapter, or by allowing genes of given relative rates of action to work for longer (or shorter) times.

The comparison of one adult form with another can be made very instructive by inscribing the shape of one form on a grid-system of Cartesian co-ordinates. If the skull of *Hyracotherium* (an early fossil regarded as ancestral to the horse) be inscribed in this way and the drawing be compared with that of the skull of the horse, it is found that the points in the horse's skull corresponding to those in that of *Hyracotherium* have been displaced. By a harmonious transformation of the grid, the skull of *Hyracotherium* can be distorted and made to resemble that of the horse. But there are intermediate steps in this distortion, and we actually have fossil horses which fit these intermediate steps perfectly (*Mesohippus* and *Protohippus*. See also p. 65). We may agree with D'Arcy Thompson when he writes: 'It is the ratio between the rates of growth in various directions by which we must account for the external form of all, save certain very minute, organisms'; and we may conclude further that it is an alteration in this ratio between the rates of growth which has produced a phylogeny such as that of the horse. It is not necessary to imply that evolution has only consisted in quantitative variation of already existing structures; on the contrary, qualitative variation in the form of structural novelties must also have appeared. But once the internal factors for these novelties have become established, they will be subject to quantitative modification and heterochrony.

It is, perhaps, worth stressing the fact that if a novelty appeared and only affected the young stages of ontogeny in a race, that race would not show any phylogenetic progression, if that is measured only by adult modification. It is therefore possible to imagine that a certain amount of 'clandestine' evolution of qualitative novelties may take place in the young stages of development while the adult stages are peacefully

undergoing quantitative changes. Such an evolution of structures in the young is well known, and called caenogenesis, or youthful adaptation. If now neoteny occurs, and the animals become sexually mature in the young condition, the phylogeny will undergo an unexpectedly abrupt modification and start off in a new direction altogether. Now, the fossil record has been of the greatest value in tracing the phylogenies of horses within the mammals, and of mammals and reptiles in general within the vertebrates; or, to take another group, of ammonites within the molluscs. But no fossils have been found which bridge the gaps between the larger groups (or phyla) of animals; between the vertebrates on the one hand and the starfish on the other, or between either of these and the molluscs or worms. Doubtless there were many forms whose fossil remains have not been found; there must have been still more which were not fossilized because they did not have any hard parts capable of being preserved. But even so, is it not possible that these gaps, that these discontinuities in the phylogenetic series of adults, may be also to a certain extent due to 'clandestine' evolution in the young stages, followed by neoteny and the sudden revelation of these hidden qualitative novelties? In the following pages an attempt will be made to show that this has occurred in some cases at least.

Attention may now be paid to those cases of phylogenies in which the modifications of successive adults appear to have taken place in definite directions. A case in point is that of the titanotheres, a group of extinct mammals. The earliest fossil titanotheres had no horns on their heads. Later fossils had horns, and in each of the four races into which the titanotheres seem to have split, these horns became progressively larger and larger, until they reached ridiculous dimensions and were probably responsible for the extinction of the race which then occurred. This incorrigible tendency to produce larger and larger horns, to vary continuously in the same direction, is an example of the phenomenon to which has been given the names of *orthogenesis* or *programme evolution*. While many authors have attempted to assign orthogenesis to the action of mysterious forces, its probable explanation in many cases has been furnished by J. S. Huxley, from a study of the relative sizes of parts of animals at different absolute sizes. In the case of the claws

of some crabs, the ratio between the size of the claw and the size of the body increases with increasing body size, or, in other words, the maximum size which the claw reaches in its development increases relatively faster than the body. Many other instances may be given of the same phenomenon, which is called *allometry* (previously known as *heterogony*). In all these cases the relative growth-rates of the allometric organ (in the case mentioned, the claw) and of the body remain constant during long periods, and may be expressed mathematically. The expression is $y = bx^\alpha$, where x is the size of the body, y the size of the allometric organ, b is a constant dependent on the particular case, and α is a constant. When the value of α is greater than 1 we have positive allometry as in the case of the claws just described; when the value of α is less than 1 we have negative allometry which is important in connexion with the reduction of organs; when the value of α is equal to 1 we have isometric growth of organ and body. The interest of this from the present point of view is that any increase in the size of the body will necessarily entail an exponential increase in the size of the allometric organ as a correlated variation, brought about by an increase in the rate of action of the factor controlling the formation of the allometric organ. Complying with this, Osborn has shown that it is a fact that the body-size of the titanotheres did increase, and that in those forms in which the horns were small they only appeared in the adult, whereas in the later-evolved forms in which the horns were large they were already present in young stages. Further, it may be concluded that unless the size of the body has reached a certain minimum value, the allometric organ will not show itself at all. So while the early titanotheres were too small to show horns, they transmitted the factors for horn-production to the four races to which they gave rise, in each of which horns appeared independently when the body became large enough. Orthogenesis of a structure in phylogeny may, in some cases, therefore, be regarded as due to the existence of a particular mathematical relation between the rate of action of the factors controlling the production of that structure and the rate of action of the factors controlling the size of the body. Lastly, it may be noticed that if an animal with an allometric organ were to decrease the size of its body, that organ would become vestigial and would finally

disappear. This has actually been proved by Champy in the case of the sword-like extension of the tail of the fish *Xiphophorus*, which becomes progressively reduced as the body decreases in size, in the adults of successive generations bred in captivity. Further consideration of these phenomena will be given in Chapter IX.



V

HETEROCHRONY AND PHYLOGENY

WE have seen in previous chapters that the strengths of the internal factors of development can vary and exert their effects at different rates, with the result that the time of appearance of a structure can be altered. It is thus possible for two organs to reverse the order of their appearance in successive ontogenies, and, by varying the rates at which animals become mature, adult structures can be reduced to a vestige and discarded, or youthful structures can become adult and so be introduced into the phylogeny. A word must be said about the term 'youthful'. From the time the egg is fertilized until the young animal emerges from the egg-membranes, i.e. hatches, it is known as an embryo, and this period is called embryonic. After hatching, and until it has assumed the adult form, the young animal is known as a larva, this period being called larval. While originally the embryonic period was very short, as animals became more complicated in evolution they took longer to develop, which meant that the time at which the young animal was hatched and could start feeding for itself was delayed. As an adaptation to this delay, a store of food was provided by the mother for consumption by the embryo in the form of yolk in the egg. By this means the embryonic period was prolonged at the expense of the larval, and structures which had been larval in previous ontogenies would (unless they were delayed also) come to be embryonic. When, therefore, it is desired to speak of a structure or character which appears in early stages of development, it may be either embryonic or larval. Which it actually is does not matter for the present purposes, and so, in order to avoid making a distinction where none is meant, in the following pages the word 'young' will be used merely to express an early stage of development, and the structures which appear at that stage will be called 'youthful'.

The distinction between adult and young, i.e. between structures which appear late or early, is drawn principally because it is the structures of the adult which form the phylogenetic

series. Now, the principle of heterochrony will make it possible for any structure to appear later or earlier as well as at the same corresponding time, when compared with a previous ontogeny. Applying this to youthful and to adult structures, we get six possibilities. A delayed appearance of new structures will mean their reduction to vestiges, unless the time at which the adult stage is reached is also delayed; whence a seventh possibility. Lastly, a distinction must be made between those youthful structures which concern only the young stage and those which persist and also affect the adult. Heterochrony, therefore, provides eight possibilities of variation in the way in which structures may appear in an ontogeny as compared with the ontogeny of the ancestor.

It is, of course, impossible to measure the relative rates of action of the factors in controlling the development of structures in the ontogenies of all animals, especially those which are extinct and known only by fossil remains. However, there is the method of comparison, for if a structure is found in the adult stage of one animal and in the young stage of another, it is obvious that the structure has developed faster in the latter. If, further, the former animal is for other reasons regarded as a representative of the ancestral type from which the latter animal descended, then it may be concluded that the phylogeny of the latter animal has been brought about by a relative acceleration in ontogeny of the rate of action of the factor controlling the development of the structure in question. All the eight possibilities outlined above may be tested in this way. It is, of course, true that the external factors can also operate in modifying the rates of action of the internal factors, but they will act on the whole more or less equally on all the internal factors, and will not, therefore, be of such importance as the internal factors in producing heterochrony. In the following considerations the external factors are regarded as constant during the phylogeny; the possible effects of their variation will be considered later.

Characters which are present or make their appearance in the young stage of an ancestral animal may in the ontogeny of a descendant appear:

- A. In the young stage only, producing youthful adaptations or *caenogenesis*, without affecting the phylogenetic adult series.

- B. In the young and adult stage, producing a substitution of a new adult condition for the old, resulting in progressive *deviation* in the ontogeny of the descendant from that of the ancestor.
- C. In the adult, by a relative retardation of the development of the bodily structures as compared with the reproductive organs, resulting in *paedogenesis* and *neoteny*.

Characters which are present in the young and adult stages of an ancestor may in the ontogeny of a descendant appear:

- D. In the young stage only, resulting in the *reduction* of the character to a vestige.

Characters which are present or make their appearance in the adult stage of an ancestor may in the ontogeny of a descendant appear:

- E. In the adult stage, resulting in those differences which distinguish individuals, varieties, and races: *adult variation*.
- F. In the post-adult stage, i.e. too late, resulting in the reduction of the character to a vestige by *retardation*.
- G. In the same stage, which is no longer adult, the new adult stage being relatively delayed, resulting in 'overstepping' the previous ontogenies or *hypermorphosis*.
- H. In the young stage, producing precocious appearance of the ancestral character and *acceleration*. The accelerated character may or may not persist into the adult stage of the descendant.

Cases B and C, which produce phylogenetic effects by introducing youthful characters into the line of adults, may be combined under the term *paedomorphosis*. Cases E, G, and H, which produce phylogenetic effects by modifying characters which were already present in the line of adults, may conveniently be included under the term *gerontomorphosis*. Cases G and H will give *recapitulatory* or *palaeogenetic* (Garstang) effects, while cases B and C will lead to results which may be described as *anti-recapitulatory* or *neogenetic*.

In the following pages examples will be given of each of the eight possibilities outlined above. Attention may, however, be called here to a point which concerns the manner in which heterochrony may have been brought about. If it be true that a structure is formed at a certain time as a result of a reaction of a certain speed, then if the speed is increased the structure

will be formed earlier. But the time of appearance of the structure may be governed not only by the speed but also by the magnitude of the reaction, i.e. by the amount of agent which

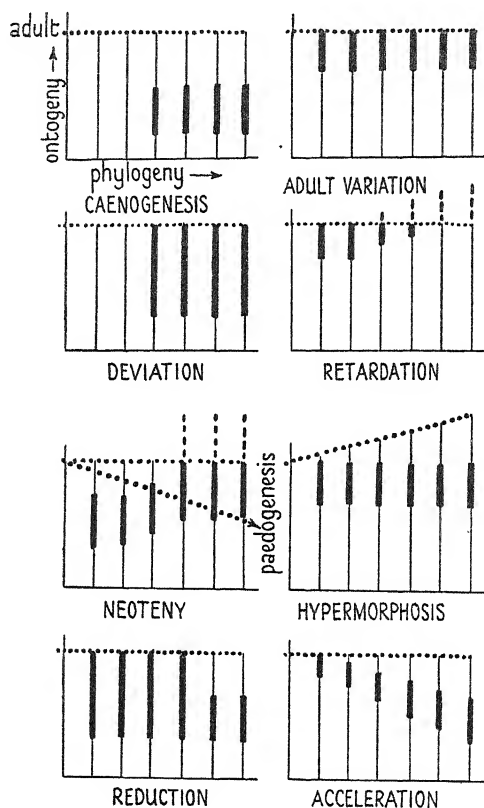


FIG. 2. Diagram of the relations of ontogeny and phylogeny. The vertical lines represent successive ontogenies; thick black denotes an evolutionary novelty.

is reacting, and this may also affect the size of the structure. It appears, therefore, to be necessary to take into consideration differences of capacity as well as differences of intensity in the reactions of the internal factors in producing structures. This is shown by the work of Ford and Huxley, who found that the condition in which the eye of *Gammarus* is pale (i.e. contains relatively little black colouring matter per unit area) can be

obtained not only by a decreased rate of deposition of the black (i.e. by decreased intensity) but also by an increase in the area of the eye (i.e. insufficient capacity). Conversely, in cases in which the area of the eye is small (as in dwarfs) a gene of low intensity has sufficient capacity to allow a rich deposit of black colouring matter, as was proved by Ford.

The time of appearance of a character will also be dependent on the time of onset of the formative processes, and Ford and Huxley have found genes in *Gammarus* which control this time. In some cases the time of appearance of a character may be delayed by the action of another factor which acts as a temporary inhibitor. The female-producing genes act as temporary inhibitors to the production of male characters in the gipsy moth up to the time at which the male-producing factors win, and the animal is switched over from one sex to the other.

It goes, of course, without saying that the time of appearance of a character must be subsequent to the time at which the reaction controlling it has been set in motion, this latter time itself being controlled by another reaction, which in turn is governed by others, starting from the moment of the fertilization of the egg, which is the time at which ontogeny begins.

It will also be understood that although we speak of characters appearing early or late in ontogeny, we do not by any means imply that they are 'unit characters', i.e. the sole effects of the internal factors controlling them.

VI CAENOGENESIS

THERE are a number of cases in which different animals resemble one another when adult, but are markedly unlike one another in the early stages of their development. These are exceptions to the 4th law of von Baer. Some of the characters which these animals have in their early stages could not possibly have been present in the adult stage of any ancestor, and so it is certain that they arose during early stages of development. This fact is important, for it proves that evolutionary novelties can and do appear in early stages of ontogeny. Here belong the cases of embryonic and larval adaptation to which Haeckel applied the term *caenogenetic*, a few of which will now be considered by way of illustration.

No one will deny that the amnion and the allantois (embryonic membranes), which are of such essential importance to the development of every reptile, bird, and mammal, could never have featured in any adult ancestral form, and must have evolved in the early stages of ontogeny. It is also worth noticing that the evolution of the mammals could not have taken place if it had not been for these embryonic novelties. It is equally certain, that the glochidium larva of the freshwater mussel (*Unio*) which is temporarily parasitic on a fish; that the larval stage of *Haemocera* which is parasitic in a worm while the adult stage is free and resembles normal Copepods; that the inflated larva of *Sitaris* which floats on the honey of the bee *Anthophora* which it parasitizes while the adult is a normal cantharis beetle; that all these youthful adaptations were introduced into early stages of ontogeny and reflect no adult characters at all.

The nauplius is a larval form commonly found in the Crustacea; the trochosphere is a larval form of frequent occurrence in Annelida and Mollusca. These forms must be regarded as larval adaptations to dispersal, and not, as recapitulationists contend, as the representatives of ancestral *adult* forms. As Woltereck has convincingly shown, the trochosphere is to be regarded as the representative of the ancestral larval form. The trochosphere could not be the form of the adult ancestor

of Annelida and Mollusca, nor could the nauplius represent the form of the *adult* ancestor of Crustacea, for that ancestor must have had its body divided into several segments, while the nauplius has only three segments. That so many Annelida and Mollusca do have a trochosphere larva is due to the fact that they have a common ancestor (which in its ontogeny had a trochosphere larva), whatever that ancestor may have been like when adult. The same conclusion applies to the nauplius. Raw has made it very probable that the protaspis is simply the larva of Trilobites, and represents no adult ancestor. These cases are not so trenchant as the amnion and allantois because they do permit of argument albeit false, whereas the amnion and allantois leave no room for argument in their interpretation.

A decisive case is, however, provided by the method of cell-division which the fertilized egg undergoes in the development of certain Platyhelminths (flat-worms), Annelida (true worms), Mollusca, and Nemertina: the method known as 'spiral cleavage'. In all these cases, the new cells are formed by division from the old cells in certain regular positions which follow a definite rule. But this rule cannot conceivably represent any *adult* feature of any ancestor; it is merely a developmental device for splitting up the single fertilized egg-cell into a larger number of smaller cells, and for sorting out the raw materials that will go to form the various regions of the future embryo.

In many cases it is possible to assert that the ontogenetic development of an organ is different from what its evolution must have been. For instance, the mammalian liver develops as a compact mass of cells permeated by bile canaliculi, subsequently penetrated by blood-vessels. But the phylogeny of the vertebrates shows that the liver was originally (as in *Amphioxus*) a simple outpouching of the gut which, in higher forms, became subdivided into a number of branches separated by blood spaces. Ontogeny here does not retrace the steps of phylogeny, but leads straight by the most direct means, as Droogelever Fortuyn has shown, to the final result.

Another excellent example, pointed out by E. S. Goodrich, is furnished by the lung. During the whole length of its phylogenetic history, the adult lung must have possessed a thin and highly vascular membrane through which gaseous exchanges took place. But in embryonic development the lung is

represented by a mass of dense mesenchyme into which the lung-buds gradually grow, followed by blood-vessels. Thus the respiratory epithelium, which must have existed at the start of the evolution of the lung, is not formed until the end of embryonic development.

Similarly, the metanephric kidney arises in ontogeny from two quite separate series of rudiments; the buds of the ureter, and the mesenchyme out of which the Malpighian corpuscles are differentiated. But in the phylogenetic series of adults these corpuscles must always have been connected with the branches of the ureter, or function would have been impossible.

Thus the embryonic development of the liver, the lung, and the metanephric kidney cannot represent any adult ancestral conditions, and must be regarded as caenogenetic innovations, evolved in early stages of development. The same is true of the mode of development of the pharynx, thyroid, and thymus in man, as Weller has shown.

Other examples of cases in which ontogenetic events are directly opposed to phylogenetic history have been given by Nauck. In the phylogeny of birds the angle between the coracoid and scapula has been reduced, and become more or less acute. In the ontogeny of the chick the angle is of 78° at 13 days incubation, rises to 138° at hatching, and drops to 64° in the adult. There is no phylogenetic background for this phenomenon, which is purely caenogenetic. Other instances are provided by the temporary and subsequently reversed embryonic changes in the retroversion of the head of the tibia, or the displacement of the bladder in man.

In most chordates the neural tube arises as a groove, the sides of which fold over to form a tube. But in *Petromyzon*, *Lepidosteus*, *Lepidosiren*, and Teleostei it arises as a solid rod, in which a canal subsequently hollows out. Clearly, one of these methods must be caenogenetic, and the same is true of the methods of formation of the lateral line canals in Chondrithyes and Osteichthyes. As Allis has pointed out, in the former the organs and lines sink beneath the epidermis and are subsequently hollowed out, and, in places, exposed to the surface. In the latter, the lines are formed as grooves and, in places, subsequently closed over. One of these methods must be caenogenetic.

It has been pointed out by de Beer that differences are found

in the causal processes and formative stimuli directly concerned in the formation of organs and structures. For instance, in the Tunicata the formation of the neural tube is not dependent on the presence of the notochord; in higher chordates it is dependent. In the frog *Rana esculenta* the formation of the lens is not dependent on the presence of the eye-cup; it is dependent in *Rana fusca*. In each case, one of these alternative methods of development must be caenogenetic.

There are many cases in which the younger stages of development of different animals are dissimilar while their adults are much more alike, though it cannot always be asserted that the youthful variations are adaptive. Hurst drew attention to the fact that while the adult forms of the insects *Culex*, *Chironomus*, and *Corethra* do not differ widely, their larval stages show much greater differences from one another. Spath has drawn attention to the same state of affairs in ammonites, and as these animals figure very largely on the platform of the recapitulationists, no evidence concerning them can be neglected. Spath states that 'as in many other ammonites, whilst the adult of *Gagaticeras* are remarkably similar, the more plastic young show great variability'. 'It is clear that a simple application of the biogenetic law to *Gagaticeras* would lead to results as absurd as in the case of a new-born monkey. To add to our overwhelming detail, while there may be pronounced rari-costation throughout several depressed whorls of young *Gagaticeras* already at a diameter of a few millimetres, in other immature specimens there is not only fine and close costation, but the whorls are round or even compressed at smaller diameters. . . . The larger whorls are almost indistinguishable. . . . Whilst we should not hesitate to identify—specifically—all the adults, ontogenetic peculiarities, such as variations in whorl-shape, might be adduced to justify the assumption of the most diverse phylogenies and skipping of hypothetical stages.'

Swinerton has pointed out that the differences between the various forms of protoconch in ammonites ('asellate', 'latisellate', 'angustisellate') do not appear to affect later ontogeny, and are examples of caenogenesis. He has also shown that the fixation of an organism like *Ostrea* to its substratum must be regarded as a caenogenetic event.

It may be remembered that Sedgwick was unable to establish

any specific difference between *Peripatus capensis* and *P. balfouri* except on the structures of the early stages of development. Other examples of cases in which the young forms differ more

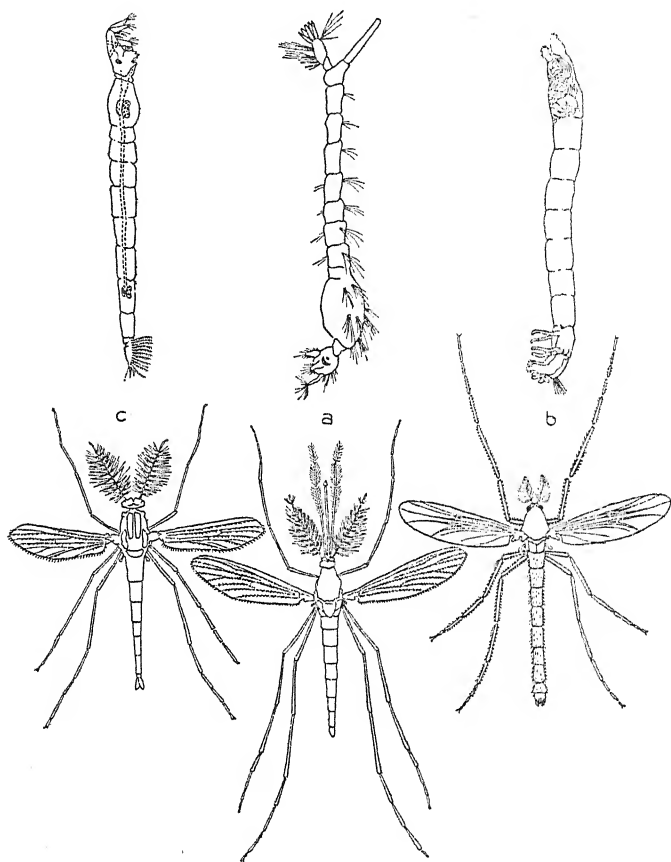


FIG. 3. The young and adult forms of three flies, to show the similarity between the adults and the differences between the young. *a*, *Culex*; *b*, *Chironomus*; *c*, *Corethra*. From Miall.

than the adults are provided by the moths *Acronycta tridens* and *A. psi*, the frogs *Rana tigrina* and *R. cancrivora*, the isopods *Chiriodotea sibirica* and *C. entomon*, the sawflies *Lophyrus pini* and *L. similis*. The nemertine *Lineus gesserensis-ruber* has two alter-

native modes of development; the fly *Chironomus salinarius* has two alternative larval forms. Buxton has drawn attention to dimorphism of eggs and larvae in several species of *Anopheles*. These cases are particularly instructive, for they show that it is possible for a certain amount of evolution to take place in the younger stages of development, without or only slightly affecting the structure of the adult stages, and therefore without producing any effect in phylogeny as commonly understood. Such evolution would then be 'clandestine'.

Some of the products of caenogenesis may be highly specialized, as in the case of the glochidium larva of *Unio*, or the parasitic larvae of *Haemocera* or *Sitaris*, mentioned above. But as we shall see later, these specialized cases are unimportant from the point of view of phylogeny, for in all probability the characters of such larvae could not figure in the adults of any descendants.

It is clear, then, that evolutionary novelties do arise in the early stages of development and may restrict their effects to those stages. It is equally clear, as Morgan points out, that the internal factors controlling the production of these novelties can be and are transmitted like any other internal factors, i.e. are genes. We therefore reach the conclusion that these youthful characters are prone to the effects of heterochrony by acceleration or retardation of the rates at which the internal factors act, and might therefore be expected to appear in the adult as well as in the youthful stages. This possibility will be considered in a subsequent chapter.

A word is, perhaps, necessary to justify the retention here of the term 'caenogenetic'. It is meant solely to designate the origin of an evolutionary novelty in early stages of ontogeny. Shorn of the implications which Haeckel attributed to it, it might seem as though the term were better dropped. But the terminology is already complicated and confused, and since the obvious alternative term 'neogenetic' is already used in another sense (see p. 95), it appears to be simplest to retain 'caenogenetic' and restrict its meaning as above.

VII

DEVIATION

IN this chapter we must consider those cases in which the young stages of development of different animals resemble one another more than they resemble the adult stages, and more than the adult stages resemble one another. We shall, therefore, have to deal with the cases which led von Baer to propose his principle of the greater resemblance between young stages, and Müller to propose the method of progressive deviation. They also form the basis of Naef's law of terminal alteration and Franz's third biometabolic mode. Sewertzow's principles of deviation and of archallaxis are also included here; the latter representing an extreme condition of the former, leading to deviation so precocious that the young of the descendant no longer resembles even the young of the ancestor. Kleinenberg's 'substitutions' are also examples of deviation. The cases considered here are of great importance because they have been used erroneously to support the biogenetic law.

One of the most interesting cases is that of the gill-slits, or rather of the gill-pouches, which appear in the embryonic stages of reptiles, birds, and mammals. These structures resemble nothing so much as the gill-slits or gill-pouches which appear in the *embryonic* stages of fish. The gill-pouches of embryo reptiles, birds, and mammals do *not* resemble the gill-slits of the adult fish. Any one who can see can convince himself of the truth of this. All that can be said is that the fish preserves and elaborates its gill-slits, while reptiles, birds, and mammals do not preserve them as such, but convert them into other structures such as the Eustachian tube, the tonsils, and the thymus glands. There is similarity between the embryos of fish and of reptiles, birds, and mammals, but the later stages of ontogeny have diverged. In the reptiles, birds, and mammals, other adult stages have been substituted for the adult stage of the fish. During the phylogeny of the reptiles, birds, and mammals, therefore, factors have arisen in the ontogenies which control the development from the embryonic stage onwards and which have produced progressive deviation.

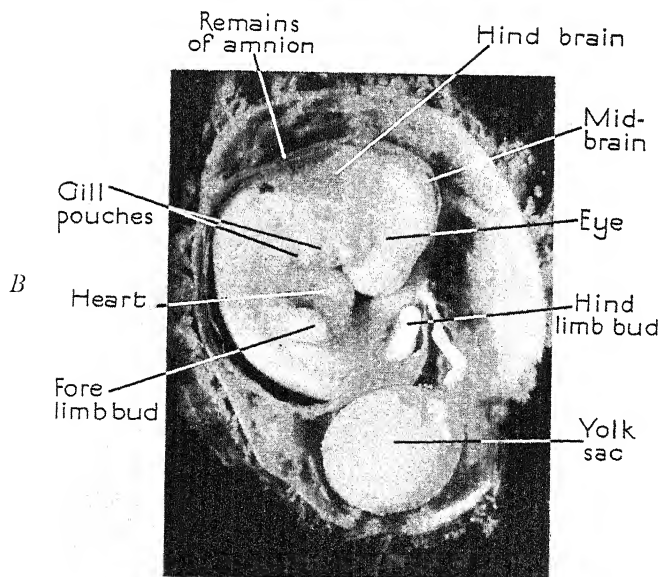
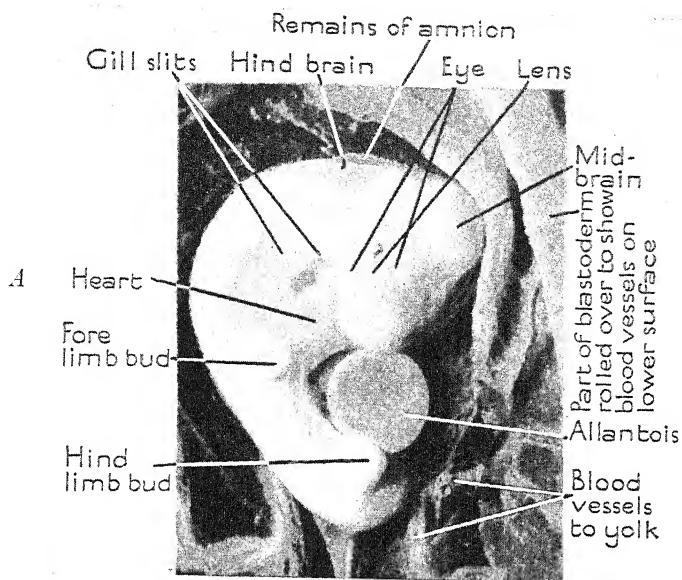


FIG. 4. An embryo of a chick (*A*) compared with that of a human being (*B*) to show the similarity between the young of animals whose adults are markedly different. After Haldane and Huxley, and by permission of Professor A. Thomson, Department of Human Anatomy, Oxford. Photograph, W. Chesterman and D. A. Kempson.

The red blood-corpuscles of mammals are nucleated before birth and non-nucleated afterwards. Lower vertebrates have only nucleated corpuscles. This does not mean that the embryonic mammalian corpuscles represent those of adult ancestral vertebrates, but simply that postnatal mammals' blood-corpuscles have lost their nuclei.

The adult stages of hermit-crabs have curved abdomens while those of normal adult crabs are symmetrical. The larval stages of hermit-crabs are symmetrical, but this symmetry surely represents that of the *larval* stages of normal crabs and not that of the adult crab. This symmetry of the larval stages of larval hermit-crabs could only represent the symmetry of the adult stage of Galatheid crabs (from which hermit-crabs are regarded as descended) if phylogeny played any part in ontogeny, and we have seen in previous chapters that there is not sufficient reason to believe that this can occur. Be this as it may, we can in another case prove that a larval form which resembles the *larval* form of another animal which is regarded as ancestral, actually differs from the *adult* form of that ancestral animal. *Portunion* is a Crustacean of the order Isopoda, and in its adult stage it is parasitic in crabs. The larval stage of *Portunion* resembles the larva of normal non-parasitic Isopoda, and like the latter, it has seven pairs of limbs on its thorax. But the normal Isopoda when they are adult have eight pairs of limbs on their thorax, and so it is definitely clear that the larva of *Portunion* takes after the larva of normal Isopoda (which are regarded as its ancestors) and not after the adult. 'It is the adult *Portunion* which has lost its legs, not the young *Portunion* which has acquired them from its adult ancestors.' (Garstang.)

Entoconcha is a member of the Gastropod order of Molluscs, and in its adult stage it is parasitic in sea-cucumbers. The larval stage of *Entoconcha* is a veliger similar to that of the larval stages of more normal Gastropoda, and so here again we find that the larval stage is a reflection of the larval stage of the ancestor and of nothing else. That *Entoconcha* and normal Gastropoda should both have veliger larvae proves only that *Entoconcha* is a Gastropod, just as a parallel line of reasoning proves that *Portunion* is an Isopod Crustacean.

The sole is a so-called flat-fish because in its adult state it has

turned over on its side and lies flat on the sea-bottom. It also undergoes a certain amount of structural modification resulting in the migration of the eye on the underside over to the upper side, and consequent asymmetrical distortion. But the larva of flat-fish is symmetrical and swims upright, and so is the larva of normal fish. The symmetry of the larva of the flat-fish corresponds to that of the larva of normal fish and only indirectly to that of the adult stage of normal fish. It is true that normal fish remain symmetrical while flat-fish become asymmetrical in the adult condition, and therefore the larva of flat-fish bears a stronger resemblance to the adult of normal fish than it bears to its own adult. But this is because the normal fish has not changed whereas the flat-fish has, in substituting its type of adult structure for that of its ancestor.

The skull of the sharks is cartilaginous throughout their life; the skull of higher vertebrates (e.g. mammals) is cartilaginous only in the embryonic stage and the cartilage is replaced by bone in the adult. This cartilaginous skull of the mammalian embryo resembles that of the embryo shark, not that of the adult shark. The essence of this fact was correctly discerned by Reichert a hundred years ago.

A very interesting case is that of the mandible of the elephant, described by Eales. During ontogeny the mandible of the modern elephant elongates until, about the time of birth, it projects some way in front of the foremost tooth. The phylogeny of elephants is fortunately well known, and there is no doubt that the ancestral elephants underwent a similar type of development of the mandible, which, up to this point, the ontogeny of modern elephants repeats. But from this point, modern elephants deviate and the mandible shortens, apparently by absorption of the anterior projection and probably by differential growth. There is therefore no evidence that it is the adult ancestral characters which the ontogeny of modern elephants repeats.

In the same way, *Antedon*, a Crinoid which is free and unattached in its adult stage, passes through a larval stage when it is attached by a stalk. Other Crinoids are attached by a stalk in their adult state, and their larvae must without any possible doubt be attached also, although they have not yet been studied. Garstang has shown that all the evidence points

to the conclusion that the larval stage of *Antedon* represents the larval and not the adult stage of its stalked ancestors.

Ammonites also provide evidence for deviation in ontogeny. The schemes of phylogeny presented by Hyatt and Würtemberger present the following situation. *Microceras densinodus* has a spirally wound shell of which the four inner whorls are smooth, the next two are ribbed, and the outer whorls are knobbed. The inner whorls are, of course, the earliest to be formed, and so the animal has passed successively through ontogenetic stages in which the shell which it made was first smooth, then ribbed, and lastly knobbed. So, on the theory of recapitulation, to quote Lang, 'it is supposed that the ancestral form had a plain shell, and that, during its evolution, the stock or lineage from which *M. densinodus* arose acquired, first a ribbed, and then a tuberculate ornament'. This example is typical of all the arguments which recapitulationists seek to base on the study of ammonites. Now, why should the ribbed-shelled stage in the ontogeny of *M. densinodus* represent an ancestral adult stage? That ancestor may have had a ribbed-shelled *early* ontogenetic stage, but there is no evidence at all of what its adult state may have been like. Indeed, in some species of *Psiloceras*, Spath has shown that the ribs make their first appearance in phylogeny in the inner whorls, i.e. in the early stages of ontogeny. After presenting further evidence of this type he concludes: 'There is no necessity for assumption of a previously existing costate stage in tuberculate ammonites, or of a slender-whorled evolute

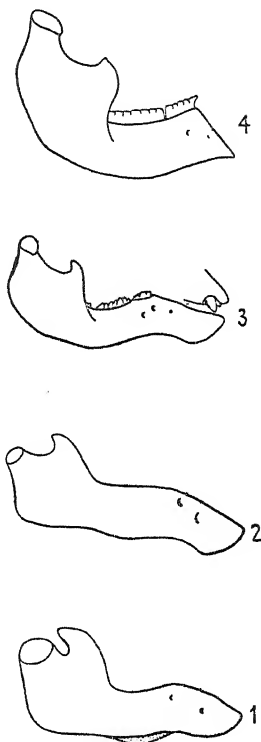


FIG. 5. The development of the mandible in *Elephas africanus* showing the reduction of the chin. 1, foetus of mandible—length 2 cm.; 2, foetus of mandible—length 5.6 cm.; 3, new-born; 4, adult. Ratio of magnifications, 30 : 12 : 3 : 1. From N. B. Eales, *Proc. Zool. Soc. Lond.*, 1931.

stage before a stout-whorled involute stage, except to make them fit arbitrary cycles and lineages; for the evidence generally points to some indifferent root, common to the two extremes.' These arbitrary cycles and lineages are based on the theory of recapitulation the truth of which is taken for granted; they do not prove it. In this connexion, it may be recalled that these lineages may involve a reversal of the geological order, which is of course absurd.

A similar conclusion is arrived at by Franz, who points out that the smooth-shelled snail *Paludina neumayri* probably gave rise in the Pliocene period to *Tulotoma*, which has ribs on the outer whorl of its shell. The inner whorls of *Tulotoma*'s shell are smooth, as are the inner whorls of the shell of *Paludina*, but none of the characters of the outer (adult) whorls of the shell of *Paludina* have appeared on the inner whorl of *Tulotoma*'s shell, although they have had all the time since the Pliocene period to do so. Ammonites and *Paludina* therefore present evidence of similarity between young stages and divergence between adults.

We may now consider a case which does not possess the value of those discussed above, because it is based on an hypothesis instead of on established fact, but it is an hypothesis which no facts contradict and which does fit all the facts consistently. It concerns the origin of the torsion of the body and shell through 180° which is so characteristic of the Gastropod Mollusca. Such a form as the limpet develops into a more or less symmetrical veliger larva which suddenly undergoes a twist through 180° , the process of torsion occupying two or three minutes. Garstang claims that there is a great advantage accruing to the larva from being twisted, for, whereas before the torsion it was not able to withdraw its head into the safety of the mantle-chamber, it can do this after the torsion. Torsion may thus be a larval adaptation, but be that as it may, Garstang has made a strong case for the view that Gastropods have twisted bodies because twisting appeared as an evolutionary novelty in the larva of their ancestor. This twisting would therefore be a caenogenetic character which differs from those which we considered in the last chapter only in that its effects persist into the adult stage instead of only affecting the larval stages of the ontogeny. This theory of the origin of the torsion

of Gastropods has two advantages. In the first place it does away with the difficulties which arise in any attempt to explain the origin of torsion on the assumption that it arose during the adult life of some early mollusc. No adaptive significance can be conceived for such an event, whereas, as we have seen, the process may be adaptive if it takes place in the larva. In the second place Garstang's theory provides an explanation for the total lack of forms showing any intermediate stages in this torsion. Torsion can take place easily in the young larva and

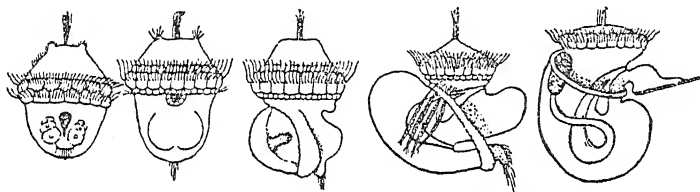


FIG. 6. Stages in the development of the limpet, showing that the animal starts symmetrical, and subsequently undergoes torsion while still young, resulting in the twisted structure which is characteristic of Gastropods. After torsion the larva is able to withdraw its head into the protection of the mantle-chamber. (From Garstang.)

twist the body of the animal through 180° at one stroke, but if it took place in the adult it would have had to take place gradually, providing intermediate stages. That intermediate stages are not *a priori* impossible is proved by the fact that intermediate stages in detorsion in later Gastropods are not wanting. There is no danger whatsoever of mistaking these detorting forms for the 'torting' forms for which we search in vain.

Next, we may consider some cases in which animals differ from others in the number of certain parts. *Nymphon* is a Pycnogonid with four thoracic segments and pairs of legs. *Pentanympyon* is similar but it has five thoracic appendages and pairs of legs. It is difficult to conceive of the extra segment and pair of legs of *Pentanympyon* having arisen gradually, for segments are either present or absent. Nor can *Pentanympyon* be regarded as the type from which *Nymphon* arose by gradual loss of a segment, for four seem to be the regular and five the exceptional number of segments in the thorax of Pycnogonids. In any case, there is still the difficulty of the change of number. There remains

the possibility that the extra segment of *Pentanympbon* was formed during the early stages of ontogeny when the material for the future thorax was divided into five instead of into four. Such a larval variation would of course affect the adult also.

Similar conclusions can be drawn from other examples. I have myself observed that in the development of the chick it is possible for the number of segments, ribs, and vertebral bodies to be greater by one whole unit on one side of the body as compared with the other which was normal. It was also plain that the discrepancy could not be accounted for by fusion of two segments on the side with the smaller number, nor by secondary splitting on the other side. It must be concluded that the process of segmentation has split up the material of the chick's body into a different number of segments on each side. In Bateson's words, there has been a fresh 'distribution of differentiation' on one side. If both sides had been partitioned as was the side with one segment too many, the animal would have been comparable to *Pentanympbon* in this respect, and formed as a result of an embryonic variation. It is possible that the extra gill-slits which are present in *Heptanchus*, *Hexanchus*, and *Pliotrema*, over and above the number which is typical in Selachians, may be explained in this way as Versluys suggests, but there are difficulties in this case.

Goodrich has shown that the position of the fins of fish has been transposed up and down the body in phylogeny, but that there is no shifting during ontogeny. The fin arises in a new position from its first appearance in ontogeny, which shows that there has been no recapitulation; instead, progressive deviation has resulted in the substitution of a new position for that of the ancestor. Sewertzow has presented similar evidence, which he uses to illustrate his principle of archallaxis.

The same phenomenon has been shown by Butler to occur in the teeth of mammals. Transitions from the pattern of typical molars to that of the teeth in front of or behind them take the same form in related species, but do not always affect the 'same' teeth ('sameness' means identity of numerical position in the jaw). It follows, therefore, that a particular tooth-type can in phylogeny move backwards or forwards in the jaws. But there is no shifting during ontogeny. The teeth arise in their new position from the start of development.

Lastly, it must be mentioned that Kryžanowsky considers *all* modifications of ontogenies in evolution to have taken the form of deviations and substitutions. He distinguishes between 'autogeneous' and 'heterogeneous' substitution. In the former, existing ontogenetic phases are partially or wholly substituted for other, earlier or later, existing phases. Here belong the cases which we have included under the headings of neoteny, retardation, and acceleration. In Kryžanowsky's second category, new phases are partially or wholly substituted for existing phases, at early, middle, or late stages of ontogeny. This category covers the cases which we include under caenogenesis, deviation, reduction, hypermorphosis, and adult variation.

The evidence presented in this chapter proves that von Baer's principles as expressed in his third and fourth laws have a wide application. The origin in the early ontogenetic stages of variations which are ontogenetically permanent (i.e. affect the adult also) is proved. These variations differ from caenogenetic variations merely in that the latter only concern the early stages of ontogeny. But this difference amounts to nothing but the lengths of time during which the internal factors controlling the variations are acting, as would result from alterations in the intensity and capacity of the factors. Nearly all the cases mentioned in this chapter have been adduced to prove the theory of recapitulation, and it has been my task to show that they do not prove it. What they do prove is embryonic similarity and repetition of characters in *corresponding* stages of the ontogenies of ancestor and descendant, which reveals the affinity between different animals, but supplies no evidence of what the adult ancestral form was like.

VIII NEOTENY

OUR object now is to consider those cases in which the adult form of an animal bears features by which it resembles the young form of its ancestors, or to put it the other way, those cases in which the young features of the ancestor have been retained in the adult stage of the descendant. Interpreting these cases in terms of heterochrony, they imply a *relative* retardation in the rate of development of the body (soma) as compared with the reproductive glands (germen), so that the body does not run through so many stages in development in the ontogeny of the descendant as it did in that of the ancestor. This state of affairs may of course be brought about in many ways, to which, in the past, different names have been given ('paedogenesis', von Baer; 'neoteny', Kollmann, 'epistasy', Eimer). As there are no hard and fast distinctions between them, they are all included here under *neoteny*. With the rate of development of the body remaining constant, this effect will be produced if the development of the reproductive system is accelerated. Here belong the well-known cases of paedogenesis, of which the most striking are those of *Polystomum integerrimum*, which has already been mentioned; of the cestode *Archigetes sieboldi*; and of the acanthocephalian *Echinorhynchus clavaceps*. The same phenomenon can be observed in *Miastor*, one of the flies. Here, the larva or grub produces the next generation without ever developing any further. Ripe germ-cells have been found in larval stages of ctenophores (*Eucharis*), scyphozoa (*Tetraplatia*), and actinians. These cases fall, however, under the heading of *dissoony*, for the organisms will become sexually mature again at the adult stage.

In other cases, the acceleration of development of the reproductive system relatively to that of the body is not so great, and we get an animal like *Amblystoma* which can become mature when it is in its larval stage, known as the axolotl. Such a case is usually called neotenous, and this one is of particular interest. The axolotl retains its external gills and gill-slits, and this is exactly what a number of other newts have done. But whereas

the axolotl is only facultatively neotenous, since it can metamorphose and assume the adult characters of *Amblystoma* under either natural or experimental conditions, *Typhlomolge*, *Necturus*, *Proteus*, &c., are permanently neotenous. There are other newts in which neoteny does not occur, and it is clear that the neotenous condition of the axolotl is an evolutionary novelty resulting from heterochrony. The same conclusion may be applied to the other neotenous forms which must have been derived from newts which only became mature after metamorphosis. The evolution of the neotenous Urodeles, therefore, has involved the retention of characters (external gills, gill-slits) in the adult stage which belonged to the larval stage of the ancestor.

Another case of neoteny is that discovered by Cousin in the cricket *Gryllus campestris*. The female glow-worm is also neotenous.

Among the Trilobites, Stubblefield has shown that the forms hitherto grouped as Proparia are most probably to be regarded as neotenous Opisthoparia. During ontogeny, the latter present a transient condition of the facial suture which is retained throughout life in the Proparian forms, which have probably evolved independently from Opisthoparian ancestors.

Comparable cases of paedogenesis or neoteny have also been found in ammonites by Smith and by Kieslinger, and in Brachiopods by Beecher.

The Appendicularians present another case which must be ascribed to neoteny. These little animals never get beyond the tailed condition that the sea-squirts pass through; the Appendicularians become mature in this state, whereas the sea-squirts and other develop further and undergo an extensive metamorphosis.

It is clear that neoteny involving acceleration of sexual maturity leads to specialization and degeneration, and is of little importance for phylogeny. On the other hand, it is easy to see that a condition of neoteny will be achieved if there is no acceleration of the rate of development of the reproductive organs, but a relatively greater retardation in the rate of development of the body. Such cases will be more interesting from the point of view of phylogeny than those described above, for if the reproductive system is accelerated, the structure of the

body will be less fully developed when the animal is sexually mature than was the body of the ancestor. On the other hand, if there is no acceleration of the rate of development of the reproductive system, but only a slower rate of succession of ontogenetic stages of the body, the latter will be no less 'well made' for retaining the larval plan. The principle here described and to be illustrated below is that to which Bolk has applied the term *foetalization*. His ideas were based on a study of human evolution, but as they may also be applied to other animals which do not possess a 'foetal' stage, it seems advisable to retain the more comprehensive term neoteny, which forms the title of this chapter. Schindewolf's term *proterogenesis* is practically synonymous with our neoteny. Garstang's term *paedomorphosis* may be applied to include phylogenetic progress by neoteny and deviation.

Bolk has shown that many of the features of the adult structure of man show resemblances to those of the embryonic structure of the anthropoid apes, and the same point of view has been expressed by Devaux. These features include the relatively high brain-weight, the position of the foramen magnum and the cranial flexure, the retarded closure of the sutures between the bones of the skull, the dentition, the flatness of the face (orthognathy), the hairlessness of the body, the light colour of the skin, and a number of other features.

The axis of the head forms a right angle with that of the trunk in the embryo of all mammals (and of nearly all vertebrates, for that matter), and this bend is known as the cranial flexure. Whereas in mammals other than man the axis of the head is rotated during later development so that the animal's head points in a direction which is a continuation of the line of its backbone, in man the cranial flexure is retained so that his head points in a direction at right angles to the axis of his body. Since the direction in which his head points, i.e. his line of sight, is horizontal, the position of the body will be vertical; and so man's erect attitude is associated with the retention during ontogeny of a condition which in other mammals is embryonic and temporary, as it must have been in man's ancestors. The erect posture of man is, in Bolk's view, a consequence of neoteny of the shape of the head.

The retention of the cranial flexure accounts for the position

of the foramen magnum, or hole in the skull through which the spinal cord enters, which position resembles that which is found in the embryos of the apes. The retention of the embryonic condition also accounts for the flatness of the human face, as compared with the elongated muzzle which is found

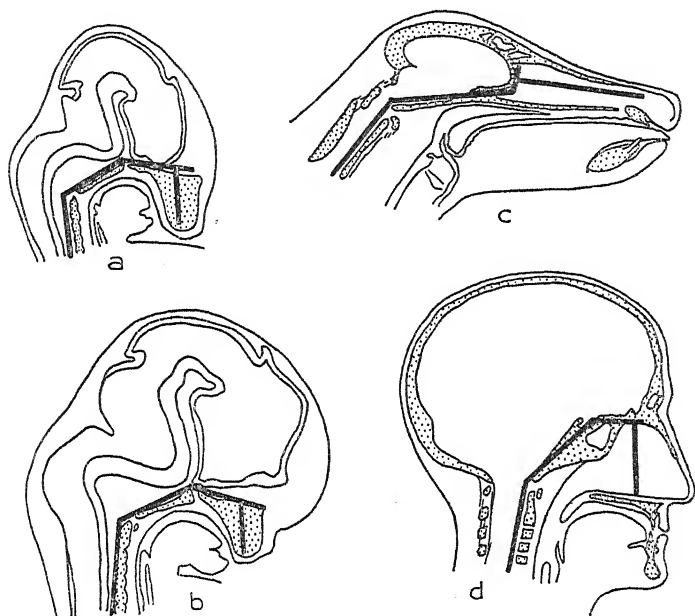


FIG. 7. A series of sections showing the angle which the head makes with the trunk in *a*, embryo dog; *b*, embryo human being; *c*, adult dog; *d*, adult human being. The embryonic curvature is preserved in adult man. (From Bolk.)

in other mammals. This feature is of importance, for a muzzle separates the eyes, and, when it is not formed and the face is flat, the two eyes can come to the front of the face and let their fields of vision overlap. This enables both eyes to be focused on one object, and Elliot Smith has shown that this development of the power of accurate vision has played an important part in the evolution of man.

The sutures between the bones of the human skull do not close until the age of nearly thirty years. In apes and other

mammals these sutures close much sooner after birth, and when that has happened the skull cannot increase in size any more. The human skull, on the other hand, can increase in size for a very long time after birth, and this enables it to provide accommodation for the large volume of the human brain. Another interesting feature is the absence of large brow-ridges (such as characterize the skulls of adult apes and of Neanderthal man) in adult man and in foetal apes. These brow-ridges are subsequent developments in the apes, and Thomson has shown that they fulfil a mechanical function in buttressing the upper jaw against a heavy lower jaw. Man is neotenous in not having developed them, the buttressing function having been taken over by the vertical wall of the forehead, and the necessity for this function having been reduced by the diminished size of the lower jaw. It is because it has no brow-ridges that the fossil Piltdown man is regarded as close to the line of modern man's descent, and Elliot Smith has pointed out that the occipital region of the Piltdown skull bears strong resemblances to that of a young ape. In this respect, young Neanderthal man presents features of great interest and similarity with adult modern man. Buxton and de Beer have drawn attention to the fact that modern man may not be unrelated to a neanderthaloid type if he can be regarded as descended by neoteny from a juvenile form of the latter.

With regard to the brain, Coupin has shown that the newborn chimpanzee resembles man more closely than does the adult chimpanzee, in respect of the relative preponderance of the different lobes of the cerebral hemispheres.

The rosy lips of man were probably evolved in the young as an adaptation to prolonged suckling, and have persisted in the adult, possibly under the influence of sexual selection.

Apes when new born have very much lighter skins than adults; additional pigment becomes deposited during later development, and the same is true of the Negro. In this respect the white races are neotenous, for they retain the embryonic condition of other forms. One of the most interesting cases of this kind is that of the hair, for Bolk has shown that a progressive series in reduction can be made out in the monkeys, apes, and man.

1. The monkey is born with a complete covering of hair.

2. The gibbon is born with the head and back covered with hair, and the other regions are covered later.
3. The gorilla is born with the head covered with hair, and the other regions are partially covered later.
4. Man is born with the head covered with hair, and the other regions are scarcely covered at all later.

It is to be noted that the lanugo, which forms a very fine covering to the unborn infant before being lost, is also present in the unborn apes. Further, the lanugo is retarded in man, for he has not completely shed it by the time of birth.

This series shows that the neoteny of man as regards hair is associated with a progressive retardation in the rate of its development. This retardation in the rate of development of the body, it will be remembered, is all that is required to produce the other human features mentioned above. It therefore becomes interesting to inquire whether the rate of human somatic development is really slow as compared with that of other mammals. That this actually is the case is proved by a table which was given in Chapter III (p. 20). Bolk has been able to give additional proof of this by a study of the development of teeth. In the apes, the milk-teeth are cut directly after birth, the 1st molar is cut soon after the 2nd premolar, and the replacement of the milk-teeth then takes place, accompanied by the cutting of the 2nd and 3rd molars. In man, the cutting of the milk-teeth is only finished two years after birth, and this is followed by a pause until at five or six the 1st molar is cut. After this, the milk-teeth are replaced, and not until this is done does the 2nd molar appear. The 3rd molar may be cut after the 2nd, but its development is often so retarded that it is not cut at all. Indeed, retardation characterizes the development of the human dentition as a whole. Associated with this retardation, as Bolk has shown, is the prominence of the human chin, for there is plenty of room for the retarded and smaller teeth and there is no necessity for the line of their sockets to protrude over the point of the chin. It is interesting to note that Neanderthal man had the simian mode of tooth-development and lacked a prominent chin.

It may then be safely concluded that the rate of development of the human body has been retarded. On the other hand, the reproductive glands have probably not varied their rate of

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development, for the human ovary reaches full size at the age of about five, and this is about the time of sexual maturity of the apes, and presumably of man's ancestors. The human body is, however, not ready for the reproductive glands to function until several years later. The retardation is due to the action of hormones, which play an important part in regulating the speed of development.

The retardation in the development of man is also associated with higher energy requirements. Rubner has calculated that in the duplication of the weight of new-born mammals of all species investigated, 4,808 calories are required for every kg. of body produced, except in the case of man, who requires 6 times as much. These figures will probably have to be corrected when experimental evidence becomes available. At all events, man's birth-weight is exceptionally low, which fact may have an adaptive significance and confer an advantage on the human female.

This case has been described fairly fully to serve as an example of the phylogenetic effect which heterochrony can produce by allowing characters which had been embryonic in the ancestor to become adult in the descendant. Two more cases will now be considered, from other kinds of animals.

Garstang was the first to look for the trace of the ancestors of the vertebrates in early instead of adult stages of invertebrates; and he focused his attention on the larvae of Echinoderms (starfish, sea-urchins, sea-cucumbers, &c.). He showed that if the ciliated bands on the larva (auricularia) of a sea-cucumber were to become accentuated and rise up as ridges leaving a groove between them, and if these ridges were to fuse, converting the groove into a tube, a structure would be produced which has all the relations of the vertebrate nervous system, including such details as the neurenteric canal. Not only this, but the two modifications of the vertebrate nervous system which are found in *Amphioxus* and all higher forms on the one hand, and in sea-squirts on the other, can be based on differences which are found in the disposition of the ciliated bands on different kinds of Echinoderm larvae. This theory of the origin of the vertebrate nervous system has several advantages. In the first place it avoids the difficulties which beset any attempt to derive it from the existing nervous systems of any

other invertebrate. It also agrees with the principle of neurobiotaxis, according to which a concentration of nervous tissue takes place in the region of greatest stimulation. If the ancestors of the vertebrates had crawled about on their ventral surfaces like most invertebrates, one would expect their nervous system to be ventral, like that of most invertebrates. But the nervous system of vertebrates is dorsal, and it is precisely the dorsal

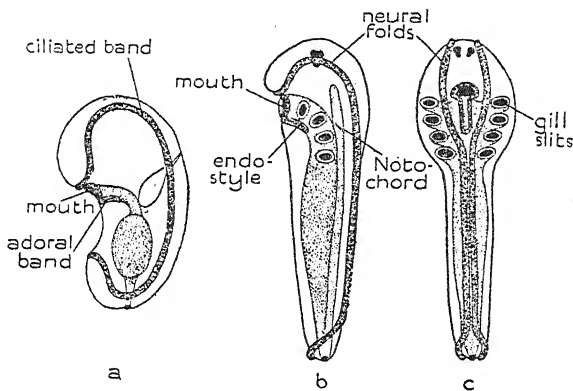


FIG. 8. A comparison between the larva of an Echinoderm (*a*) and the form of a typical primitive Chordate (*b* and *c*). The bands of cilia of the former correspond exactly to the neural folds of the latter, as do the adoral band and the endostyle. *a* and *b*, side view; *c*, dorsal view. (After Garstang.)

side of the body which would receive the greatest stimulation in a form swimming freely in the sea, the stimuli being the rays of light penetrating through from the surface. Not only is the auricularia free-swimming, but it bears an unmistakable resemblance to the tornaria larva of *Balanoglossus*, and *Balanoglossus* is an undoubted relative of *Amphioxus* and the early vertebrates (or chordates as they may more correctly be termed). But the resemblance between the Echinoderm larva and the chordate goes further still, for the former has an adoral ciliated band formed partly from the inner layer of the body; and in a corresponding position the chordates have a ciliated band called the endostyle, which is looped in the same peculiar manner as the other. The middle layer of the body arises in three tiers or segments in the Echinoderm larva and in *Balanoglossus*, and indications of this tripartite arrangement are present in

Amphioxus. Further, the body-cavity of the Echinoderm larva is in communication with the outside by a pore, as in *Balanoglossus*, *Amphioxus*, and several other chordates. In fact, if the nervous system and endostyle are formed in the way suggested, all that is required to turn the Echinoderm larva into a chordate is the formation of the notochord and the piercing of the gill-slits.

Now the Echinoderm larva undergoes an extensive metamorphosis, during which the general larval form and symmetry are lost, and it becomes the adult starfish, sea-urchin, or sea-cucumber, as the case may be. Their adult structure is so special and peculiar that no one would dream of regarding the adult form of any Echinoderm as ancestral to anything at all. Nor indeed is it proposed that the chordates were derived from the larvae of Echinoderms as they now are. But there must have been animals whose adults were less special and peculiar than the adults of existing Echinoderms, and whose larvae resembled those of existing Echinoderms. If, then, the larval form of these animals persisted and they became sexually mature in this state, such neotenous forms would provide exactly the necessary material for the evolution of the chordates on the lines suggested. Indeed, the general form and symmetry of the tornaria do persist when this larva develops into the adult *Balanoglossus*.

Next, we may turn to the comparison which may be drawn between the adult form of the insects and the larval form of certain Myriapods such as *Iulus* (the millipede). The body of the adult insect consists of a head which is made up of six or seven segments, some of which bear jaws; a thoracic region of three segments each of which bears a pair of legs; and an abdominal region of about ten segments which usually do not bear any legs. Now, the larva of *Iulus* hatches as a little animal with a head which seems to be composed of the same number of segments as that of the insect, and a body of roughly a dozen segments of which the first three each bear a pair of legs. The 4th and following segments of the body are not devoid of legs but they are retarded in development and so small that they do not protrude far, as Metschnikoff showed. This six-legged larva of *Iulus* eventually develops into an elongated adult form composed of several segments and bearing many legs. Now, if the retardation in the development of the legs

behind the first three pairs were increased, and the larval number of about a dozen body-segments persisted into the adult stage, there would be formed an animal like an insect with the legs behind the first three pairs either reduced to vestiges or vanished altogether. It is therefore of interest to find that there actually are insects in which vestigial legs are present on the abdominal segments (*Campodea*, *Iapyx*, *Machilis*). These insects have no wings, and on the other hand have

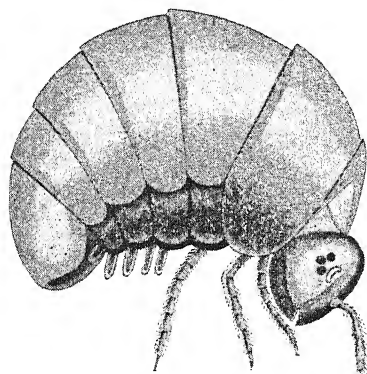


FIG. 9. The larval form of a Myriapod soon after hatching, showing its great resemblance to an Insect. (From vom Rath.)

preserved features which the other insects have lost (such as the segmental arrangement of the reproductive glands), and they may therefore be regarded as an intermediate stage in the process of heterochrony, and of the evolution of the insects from neotenous larvae like those of the Myriapoda.

The derivation of insects from forms like Myriapoda is supported by many other considerations. To start with, the insects must have been derived from forms which possessed longer bodies with more segments and legs than the insects now have, for, in common with Myriapoda, Crustacea (lobsters), Arachnida (spiders), and the Peripatoidea, the insects must ultimately have been derived from worms. Of all animals with long bodies and many legs, the Myriapoda are the most likely to have been the ancestors, or closely related to the ancestors, of the insects, for they have several features in common. Such, for instance, are the tracheal tubes and Malpighian tubes of the

respiratory and excretory systems respectively. At the same time, insects could not have been derived from adult Myriapoda, for the structure of the latter is too specialized and peculiar.



FIG. 10. Introduction of an evolutionary novelty (reflexed theca) in the first-formed members of the Graptolite *Monograptus argenteus*. Arrows indicate the directions of the thecal apertures. (From O. M. Bulman, *Biol. Rev.* 8, 1933.)

Neoteny need not, of course, affect all structures of the body, and may be restricted to quite few. A case of this kind is provided by the plumage of the ostrich and other flightless birds and penguins, which resembles the nestling down of young nidicolous birds. Far from meaning that the ostrich is primitive and that its plumage is 'recapitulated' in the ontogeny of a bird like a fowl, this series must be read exactly the other way. Steiner's morphological researches establish beyond doubt that the nestling down feathers are derived from quill feathers, and Hosker's embryological studies show that the former are merely the precociously formed and fluffed out tips of the latter. It is clear, therefore, that the ostrich, in retaining in the adult a type of plumage characteristic of the young of other birds, is neotenuous. This accords perfectly with the now generally accepted view that the flightless birds were evolved from birds with well-developed power of flight, and have therefore lost their flight feathers.

The ammonites also call for mention here, for Spath has found that characters may make their first appearance in phylogeny at early stages of ontogeny and subsequently extend into adult stages. Berg cites other examples of this phenomenon in ammonites discovered by Pavlov. Similarly, in Graptolites, Bulman has drawn attention to the fact that 'it is the initial thecae which exhibit the first signs of incoming developments'. That is to say, these evolutionary novelties appear first in early stages of ontogeny and become prolonged into later stages in subsequent phylogeny; this notwithstanding the fact that in some other characters (change of direction of growth, delayed bud-formation), the

evolutionary novelty first affects the terminal parts of the stalks on which the thecae are borne.

An excellent example of neoteny has been pointed out by Schindewolf in Nautiloids. *Rhynchorthoceras* has a straight shell, and is succeeded by *Ancistroceras* and *Lituities* in which the proximal (i.e. young) end of the shell begins to coil. This is

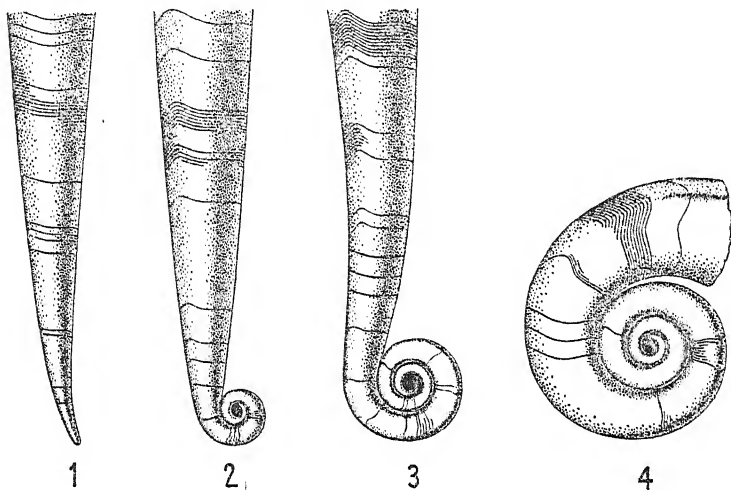


FIG. 11. Neoteny in Nautiloids. 1, *Rhynchorthoceras*; 2, *Ancistroceras*; 3, *Lituities*; 4, *Cyclolituities*. (From O. H. Schindewolf, *Acta Biotheoretica*, 3, 1937.)

followed by *Cyclolituities* in which the coiling extends to the distal (i.e. adult) end of the shell

On looking back over this chapter, we may say that there are a number of cases in which the adult structure of an animal resembles the embryonic or larval structure of another animal, and in each case there are good reasons for regarding the former as having been derived from the latter. If the neotenuous condition is achieved by accelerating the rate of development of the reproductive glands and hastening the time of maturity, the phylogeny usually results in a simplification often associated with parasitism. But if the neoteny is brought about by a slowing down of the rate of development of the body relatively to that of the reproductive glands, then changes are brought about which may have considerable importance in phylogeny.

IX

VESTIGIAL STRUCTURES DUE TO REDUCTION

WE shall deal in this chapter with those cases in which a character, which in the ancestor was present in both young and adult, comes in the descendant to be either very reduced or absent in the adult and therefore present only in the young stages. These cases really constitute the other side of the picture presented by deviation. In deviation, as we have seen, a character appears in the ontogeny and often substitutes itself for a previously existing character. The latter character thus becomes suppressed, reduced, and vestigial. In this way we may say, reverting to the example of intersexuality in the gipsy moth, that the female characters become vestigial in the adult of a female moth which during its early stages of development has been switched over to maleness. This, as we have seen, is due to the relatively lower rate of action of the female-producing genes. Consequently, we may ascribe the cause of the reduction of structures to vestiges to a quantitative decrease in the intensity and capacity of the internal factors controlling the formation of those structures. If the structures are related to the size of the body and are positively allometric (p. 25), then if the size of the body decreases during phylogeny, the structure in question will be reduced. The case of the tail of the fish *Xiphophorus* described in Chapter IV (p. 26), is an example of this type of reduction. Conversely, if the structures are negatively allometric, they will be relatively reduced if body-size increases.

The following examples of reduction may now be given.

The frog tadpole possesses a tail, which is a characteristic chordate structure, of universal occurrence in the young. But whereas most chordates preserve their tails in the adult state, the adult frog is tailless.

The young oyster has a foot, like the young of other shell-fish. But whereas the latter preserve the foot in the adult state, the oyster loses it. The abdominal limbs, which in the larval stage of the Myriapod *Iulus* are small but become fully developed in



FIG. 12. Reduction of an allometric structure—the tail of *Xiphophorus helleri*—accompanying reduction in body-size. From C. Champy, 'Sexualité et hormones'. (G. Boin, Paris, 1924.)

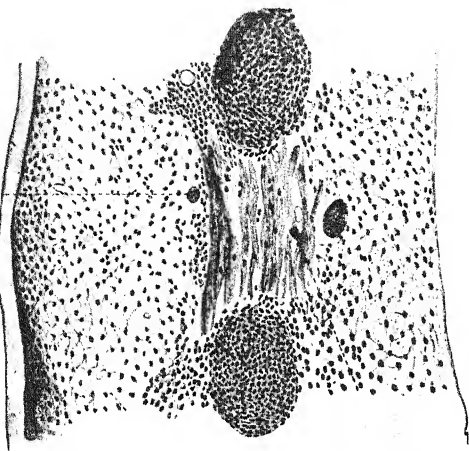


FIG. 13. The intercostal muscles of an embryo of *Emys lutaria* prior to their reduction. From A. N. Sewertzow, *Zool. Jahrb. Abt. Anat.* 53, 1931.

the adult, remain small in the adult *Campodea*, *Iapyx*, and *Machilis*, as vestiges, and in other insects they are reduced altogether. In early stages of development, the slow-worm (*Anguis*) has small limbs, and so has the early stage of the lizard. But whereas in the latter these limbs go on developing and are present in the adult, in the slow-worm they do not develop any further and eventually disappear, so that the adult is limbless. This reduction goes still further in snakes, where, with the exception of the *Python* and *Boa* which still show a trace, the limbs never arise at all.

Huxley has drawn attention to the importance of allometric growth studies in this connexion. If, as appears to be the case, the initial steps in the reduction of a structure involve decreases in the activity-rates of growth-controlling genes resulting in negative allometry, the mere fact of the existence of limb rudiments in the embryo slow-worm is no evidence of any recapitulation of adult ancestral characters; it is evidence of the repetition of embryonic characters which the organism is going to get rid of by what may perhaps be the only means at its disposal: negative allometry.

Further, it may be noted that as the size of an allometric organ is related to that of the body, the absurd degree of reduction of some organs, such as the hind limb of whales, can be accounted for quite independently of the question of the function that such organs could possibly perform.

The notochord (primitive spine) arises in early stages of development of all chordates, but while in *Amphioxus*, lampreys, some fish, and newts it persists more or less into the adult, in reptiles, birds, and mammals it is reduced and replaced in the adult by the vertebral column. Franz has emphasized the fact that the notochord of the embryo of these higher vertebrates does not resemble that of the adult *Amphioxus* or sturgeon, but rather the notochord of the early stages of development of these animals. The possession of these vestiges is therefore no evidence of the pressing back of adult ancestral characters into the young stages of the descendant. The same is true of the tooth-band and small teeth which are found in the embryos of the whale-bone whales. These animals are toothless in the adult, and their embryonic teeth represent the embryonic condition of other mammals. Other examples are the 3rd toe of the young

ostrich, while its adult has only two, the 3rd toe persisting in the adult stages of other birds; the rudiments of the intercostal

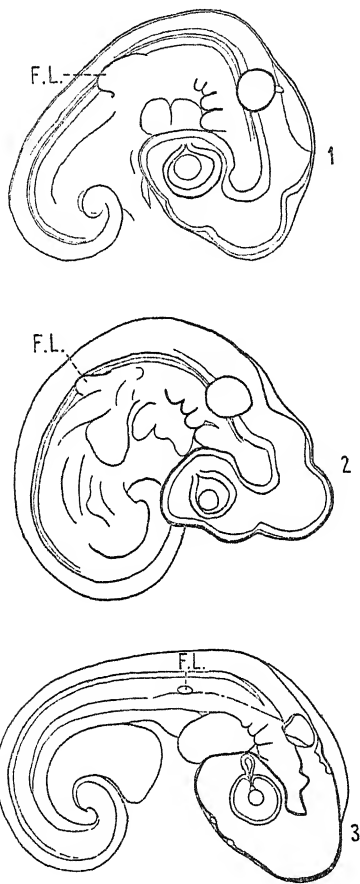


FIG. 14. Embryos of 1, *Ascalabotes fascicularis*; 2, *Seps chalcides*; 3, *Ophisaurus apus*, showing reduction of the rudiment of the forelimb, F. L. (From A. N. Sewertzow, *Zool. Jahrb. Abt. Anat.* 53, 1931.)

muscles which the Chelonian *Emys lutaria* has in its embryo but loses in the adult, while adult non-chelonian amniotes retain them; the rudiment of Jacobson's organ in embryonic man who loses it in the adult stage, while it is present in other adult mammals; and the rudiment of the head-kidney or pronephros which is formed in the embryonic stages of all chordates, persists in the adult of some fish, but is lost in the adult of all other forms.

Sewertzow has analysed the processes of reduction and found that they conform to one of two types. In the first, 'rudimentation', the embryonic rudiment of the organ in question is smaller throughout ontogeny as compared with the corresponding organ in more normal forms. Examples are provided by the lizards *Seps chalcides* and *Ophisaurus apus*. In these cases the vestigial organs are functionless. In the second type, 'aphanisia', the organ in question develops as in more normal forms up to a certain point and is then rapidly destroyed.

Examples are the tail of the frog tadpole and the intercostal muscles of *Emys*. In these cases the organs are functional up to the time of their loss. 'Rudimentation' seems to involve

reduction in size of the presumptive organ-forming regions and negative allometry; 'aphanisia' is brought about by phagocytosis, humorally controlled involution, and histological degeneration.

The effect of reduction from the point of view of phylogeny will usually be to produce changes of relatively small systematic importance. This is, however, not always the case, and, as Goldschmidt has pointed out, the reduction of the hyomandibula of the fish to form the columella auris or stapes of higher vertebrates was an evolutionary change of great importance.

We see, lastly, that as in the case of deviation, the instances in which structures are reduced to vestiges obey von Baer's law of the greater degree of resemblance that exists between young stages of different animals than between young and adult stages or between adult stages *inter se*.

X

ADULT VARIATION

UNDER this heading we include what is really only a special case of the phenomenon which was described under the term deviation. As has been stressed before, the reactions which result in the appearance of characters are set going some time before those characters appear. The adult form is being prepared during the earlier stages of development. We cannot draw any hard and fast line between the characters which, substituting themselves for others in phylogeny, appear early in ontogeny, and those which appear late. However, the later a character appears in ontogeny, the smaller as a rule is the change which it produces by its presence. On the other hand, a character which appears early in ontogeny has time to produce more important changes. So, while under the heading of deviation we include variations which have produced fairly large phylogenetic effects (such as the divergence in evolution between different families, orders, and classes of animals), adult variation deals with the differences between individuals, varieties, races, and, probably, species. Darwin himself drew attention to the fact that 'slight variations generally appear at a not very early period of life'.

It is of course not denied that some trivial characters may appear early in ontogeny. For instance, right- or left-handedness in the asymmetry of snails is determined in the ovary of the previous generation and manifested at the first cleavage division of the fertilized egg, but the results do not even confer specific distinction. Cope cites cases in which the appearance of specific characters precedes that of generic characters. What is contended, however, is that systematically important characters do not arise late in ontogeny.

To this chapter, then, belong the slight differences between animals, and genetic research tends increasingly to show that these differences are controlled by Mendelian factors or genes, and that they may concern any and every feature of an animal. No useful purpose would be served by going more fully into them. The substitution of one character for another in the adult does

not usually involve heterochrony, and produces only small phylogenetic effects. Just as, however, caenogenetic variations may become phylogenetically important by undergoing heterochrony, attention must be paid to the possible results of heterochrony if applied to adult variation, and this will form the subject of the following chapters.

XI

VESTIGIAL STRUCTURES DUE TO RETARDATION

WHEN, as in neoteny, characters which had been larval or embryonic in the ancestor become adult in the descendant, the original adult characters of the ancestor tend, as it were, to be pushed off from the end of ontogeny. They arise too late to be fully formed by the time maturity is reached in those animals which have a definite adult form, and, in consequence, such characters become reduced and vestigial. Retardation of structures to vestiges is therefore the other side of the picture presented by the phenomenon of neoteny. Hair is vestigial on the body of man, as are the molars, especially the last, which are often not cut at all. The bones are vestigial in the skull of the axolotl, and the maxillary bone, which is present in the newts which undergo metamorphosis to the terrestrial adult form, is absent in those Urodeles which are permanently neotenous.

A very instructive case of retardation is that of the bands on snail shells investigated by Diver. These bands vary considerably in the time in ontogeny at which they make their appearance on the shell. Some may be so late as to appear as a mere dot just behind the terminallip of the shell. 'Others may even be, as it were, pushed off the shell altogether, that is they fail to appear at all because their time of appearance has been so retarded in relation to general development that growth is terminated before they are due.'

It is possible to interpret these cases in terms of the phenomenon of intersexuality in the gipsy moth by noting that in a normal female moth, the male-producing genes are too slow to produce the appearance of any male characters before the time of maturity arrives and development ceases. Characters may become vestigial by the over-retardation of the rate of action of the factors which control them. The effects of such heterochrony will not in themselves be important in phylogeny, but they will be associated with neoteny, and this, as we have seen, may and often does have important results in evolution.

XII

HYPERMORPHOSIS

IF those characters which only appear in the adult stage of the ancestor are retarded so that they do not appear in the descendant by the time development ceases, they will become vestigial, as shown in the previous chapter. But if the time when development stops is *relatively* delayed, it will be possible for the descendant to add characters on to the adult ancestral stage. Referring again to the example of intersexuality in moths, male characters do not normally appear by the time development ceases, but if the time of maturity is postponed, these male characters can and do make their appearance. This additional development, or *hypermorphosis*, may then be expected in cases where the evolution has resulted in progressive increase in size, or where the time of maturity is delayed relatively to the body characters. The cases to be considered here conform to the principle of 'overstepping' of Müller, of 'prolongation' as suggested by Franz, and partly to the principle of 'anaboly' as enunciated by Sewertzow.

An instructive example is that of the skull of the horse, studied by Robb. During phylogenetic evolution from *Hyracotherium* to the modern percheron, the ratio of face-length to cranium-length has doubled. This ratio is a direct function of total size, and face-length follows the principles of allometric growth (p. 25), according to the formula

$$\text{face-length} = 0.3 \text{ skull-length}^{1.2}$$

But the ontogenetic development of the modern percheron shows exactly the same growth phenomena. The ratio of the dimensions of the skull of a 5 months' foetus corresponds to those of adult *Eohippus*. The growth mechanism has been the same throughout horse phylogeny, and since the shape of the skull is determined by its size, the progressive increase in size which has accompanied the evolution of the horse brings it about that the modern horse in its ontogenetic development passes through and beyond the skull-forms of its adult ancestors.

Other examples are given by Huxley. The limbs of lambs of domestic breeds pass through stages in which their proportions

correspond to those of adult wild (and therefore presumably ancestral) sheep. Schultz's demonstration of the lengthening of the arm of the gibbon during ontogenetic development reflects the lengthening that must have occurred in the phylogeny of gibbons from anthropoids whose arms were of more normal length.

This case is particularly interesting, because the same phenomenon, the lengthening of the arms during human ontogenetic development, clearly does not reflect man's phylogenetic evolution from brachiating ancestors, during which the length of his arms has been reduced.

The apparent recapitulatory effect in the cases of the horse's skull, the sheep's limbs, and the gibbon's arm are simple consequences of the values of the growth constants. A change in these values immediately produces a very different state of affairs. For instance, in the horse the growth-rate in ontogeny of the splint bones does not reflect the changes in size of the lateral digits of the 3-toed horses in phylogeny, as Robb has shown. This case and that of man's arm show caenogenesis, producing an anti-recapitulatory effect.

The caution needed in interpreting these cases is well illustrated in the evolution of Gryphaean oysters. Trueman has shown that the hinge of the left valve of the shell undergoes progressive spiral coiling in phylogeny. The descendants show not only additions to the coils of the ancestors, i.e. hypermorphosis, but the coil itself becomes tighter. Thus the angle of the coil in *Gryphaea obliquata* increases in ontogeny to a value of 60° in late stages. In the descendant *G. incurva*, this is the value of the angle at early stages, rising to 80° at late stages. Here, therefore, we have hypermorphosis combined with acceleration, producing a recapitulatory effect.

Turning now to other examples, *Achtheres* is a crustacean belonging to the Copepoda, which in its development passes through a so-called 'copepodid' stage, in which it only differs from a normal adult copepod in that the segments of its thorax are not so clearly marked, and its limbs are fewer and smaller. The adult *Achtheres* as the result of further development is parasitic and degenerate. Another comparison of the same sort might be made between the adult *Mysis* (the 'opossum'

shrimp) which has forked legs, and the so-called 'mysis' stage in the development of the lobster. The adult lobster has lost one of the prongs of each of the originally forked legs.

Sewertzow's principle of anaboly is a modification of that of 'overstepping'. In the ontogeny, Sewertzow distinguishes an earlier period of morphogenesis during which the various structural characters of the developing animal are moulded, and a later period of growth in which the animal increases in size until it reaches the adult state without undergoing further modification. He regards it as possible for a descendant to add a new stage on to the last stage of morphogenesis of the ancestor. As an illustration of this principle we may take the development of the long-snouted fish *Belone*. In the adult, *Belone* has both the upper and the lower jaw very much elongated, but in early stages of morphogenesis its jaws are both short, as in the final stage

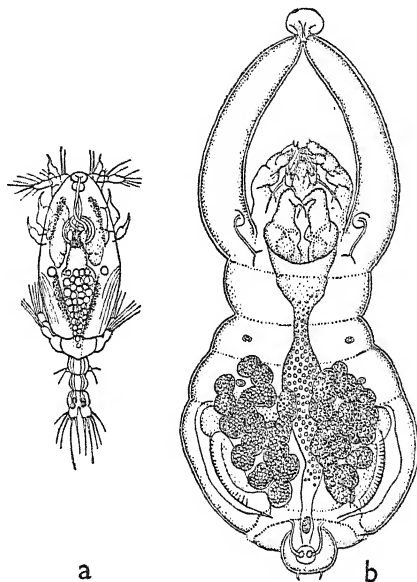


FIG. 15. *Achtheres percarum*. a, 'copepodid' stage; b, adult. After W. T. Calman, *Crustacea*, A. & C. Black, London, 1909.

of morphogenesis of such a fish as *Exocoetus*. At a later stage, the lower jaw of *Belone* elongates greatly, producing the appearance which is presented by the final stage of morphogenesis of another fish—*Hemiramphus*. Lastly, the upper jaw of *Belone* also elongates to produce the long-snouted condition of its final stage of morphogenesis, which then enlarges by growth without further modification to form the adult. It will be noticed that Sewertzow's anaboly differs from 'overstepping' only in that it is the final stage of morphogenesis instead of the definitive adult stage of the ancestor which is passed through in the ontogeny of the descendant. But in either case, the stage

which the descendant passes through is the final stage of 'development' of the ancestor, for development, i.e. structural alteration, does not take place during Sewertzow's period of growth.

At all events, both Franz and Sewertzow lay stress on the fact

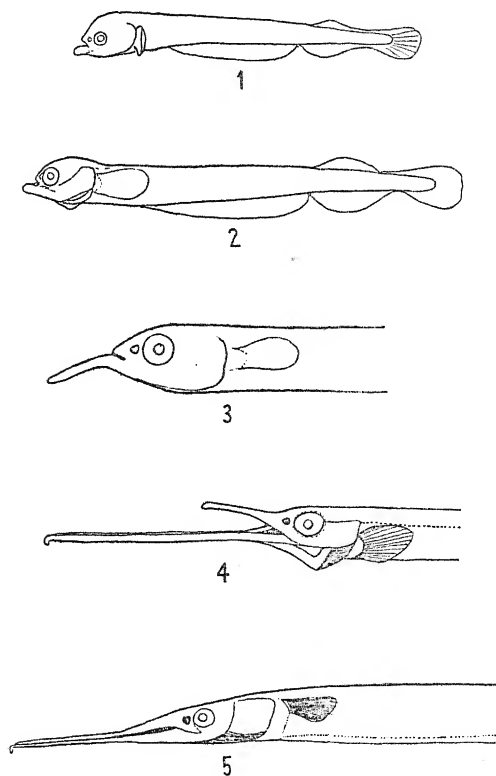


FIG. 16. Development of *Belone acus*. 1 and 2, young stages resembling *Exocoetus*; 3 and 4, intermediate stages resembling *Hemiramphus*; 5, adult *Belone*. From A. N. Sewertzow, *Jena Z. Naturwiss.* 63, 1927.

that the adult stage or final stage of morphogenesis of the ancestor is not pressed back into earlier stages of development in the descendant, but the ontogeny or morphogenesis of the latter is prolonged. The adult condition or final stage of morphogenesis of the ancestor is present unreduced in the development of the descendant, but it is no longer the terminal

stage of ontogeny or morphogenesis. With this reservation, cases of hypermorphosis may be said to conform to Haeckel's principle of the recapitulation of adult (or final morphogenetic) stages in the ontogeny of the descendant. It is to be noted that such recapitulation is not as its name would imply an abbreviated (i.e. accelerated) repetition, but a simple repetition.

Here we may draw attention to the value of hypermorphosis in providing an explanation of some cases of the widespread phenomenon which Barcroft has called 'anticipation', i.e. the formation of a structure in anticipation of its use. The haemoglobin of a mammalian foetus is adapted to placental intra-uterine respiration, and differs from the haemoglobin of a post-natal mammal, adapted to pulmonary atmospheric respiration. The transition from one type of haemoglobin to the other takes place at birth in man, but before birth in the sheep. If the period of gestation of the sheep has been prolonged, as is not improbable in view of its well-developed state at birth, but the time of transition of the haemoglobins remained unaltered, this 'anticipation' in the sheep would be explained. But even the case of man and other mammals which change their haemoglobins at birth is anticipatory in the sense that it is the result of processes antecedent in time to the realization of the adaptive value of the change. It might be expected that in the ancestors of the mammals the change in haemoglobins took place after birth or hatching, and it is therefore of great interest to note that in the chick, Hall has found that the change is not completed until 6 weeks after hatching.

In a sense, of course, the problem of 'anticipation' is that of all embryology during the prefunctional period, when organs are formed, seemingly teleologically, 'in order to function' later. It would be more than rash to conclude that all cases can be explained as the one above, especially as so many developmental processes can be proved to be caenogenetic innovations which cannot have any ancestral adaptive significance. Nevertheless, there are probably many cases of physiological anticipation which might well repay comparative study from the point of view of hypermorphosis.

It must be admitted that part of the evidence for the principle of hypermorphosis rests on the assumption that a normal adult copepod was ancestral to *Achtheres*; that a normal adult *Mysis*

was ancestral to the lobster; and that fish whose final stages of morphogenesis, and therefore whose adults, were like those of *Exocoetus* and *Hemiramphus* were ancestors of *Belone*. But is there any evidence of this? It is equally possible that normal copepods and *Achtheres* had a common ancestor from which each have diverged, and the copepodid stage of *Achtheres* would be evidence of affinity with normal copepods. Similarly, *Mysis* and the lobster may have had a common ancestor which gave rise to both, the mysis stage of the lobster showing its affinity to *Mysis*. In the same way, a common ancestor may have given rise to *Exocoetus*, *Hemiramphus*, and *Belone*, the ontogenetic stages of *Belone* betraying its affinity to these fish.

In the process of these phylogenetic divergences, *Achtheres* may be regarded as having developed farther than normal copepods; the lobster farther than *Mysis*; *Hemiramphus* farther than *Exocoetus*, and *Belone* farther than *Hemiramphus*. There is no necessity for regarding these forms as all on one and the same line of descent. In other words, these instances may just as well, if not better, be regarded as illustrating the principle of progressive deviation, dealt with in Chapter VII. If this is so, there is then no justification for the view that adult or final stages of morphogenesis of any ancestors are included in the ontogeny of *Achtheres*, the lobster, or *Belone*. Instead, these cases would serve as an illustration of the principle to which Eimer gave the name 'epistasy', according to which, of two related forms, one might undergo more modification in ontogeny than the other.

Nevertheless, repetition by hypermorphosis is apparently possible as the result of heterochrony and prolongation of the period of development, as the other cases mentioned in this chapter seem to show. And while they appear to support Haeckel's theory of recapitulation, it must be remembered that the adult ancestral characters are not compressed into earlier stages of the development of the descendants in hypermorphosis. It may also be noticed that the phylogenetic effect that hypermorphosis may produce is not great.

XIII

ACCELERATION

WE have now to consider the last of the possible results that heterochrony may produce. By acceleration of the rate of action of the internal factors which control its formation, a character which appeared in the late features of ontogeny of an ancestor may appear early in the development of a descendant. Swinnerton's term 'deutero-genesis' applies to those cases in which the character in the adult descendant is farther developed than in the adult ancestor, owing to its acceleration. In other cases, the accelerated character may no longer appear in the adult stage of the descendant. The embryonic or larval features of the descendant may then resemble the adult stage of the ancestor. The conditions required for Haeckel's theory of recapitulation will then be fulfilled, but again with the remark that accelerated repetition of a character in the ontogeny of the descendant does not constitute a pressing back of a complete ancestral adult stage into an earlier period of ontogeny. The following examples of acceleration may now be considered.

It is not always easy to be certain that a case which appears to show acceleration is not really one of hypermorphosis. This is especially true when the character in question is associated with a shell formed by successive increments. Acceleration and hypermorphosis are, of course, not mutually exclusive, for in the evolution of *Gryphaea*, as we have seen (p. 66), the angle of the coil of the older part of the shell of the ancestor is reproduced in the younger part of the shell of the descendant.

A case in many ways analogous is provided by the Foraminifera. The inner whorls of the coiled shell of *Cyclocypeus* repeat the formation of chambers characteristic of the probably ancestral form *Heterostegina*, as Tan Sin Hok has shown. But the number of these heterostegine chambers diminishes in successive species of *Cyclocypeus* from 38 in the Oligocene to 3 in the Pleistocene.

The corals of the genus *Zaphrentis* provide a good phylogenetic series of which the later stages of ontogeny are also known. The series runs from *Z. delanouei* through *Z. parallela*

and *Z. constricta* to *Z. disjuncta*. It is found that the penultimate stages of ontogeny of each of these species resemble the ultimate stages of the immediately preceding species in each case. If hypermorphosis is not at work here, *Zaphrentis* can be taken as a good example of acceleration. At all events, the effect is recapitulatory, although, as Swinnerton has shown, other characters of *Zaphrentis* show deviation.

Although the protaspis stage of Trilobites appears to be caenogenetic, the later stages of their ontogeny show acceleration, for Raw claims that these stages in *Leptoplastus salteri* recapitulate the conditions in *Ctenopyge*, *Parabolina*, and other presumed adult ancestors.

Acceleration is claimed to occur in ammonites by Smith and in Brachiopods by Fenton, among other authors. But it is not always clear that the ancestral characters repeated were those of ancestral *adult* rather than young forms (i.e. cases of deviation), while many examples appear to conform to hypermorphosis.

One of the most interesting features of the very early stages of development of the chick is the precocious formation of the heart. Indeed, the heart may almost be said to arise and to enter upon its functions before the embryo itself is there. In the development of lower forms such as the frog, for instance, the general form and architectural plan of the embryo is fully marked out by the time the heart appears. There can, then, be no doubt that in the chick the formation of the heart has been accelerated relatively to the rest of the body. The 'reason' for this precocity in the formation of the heart is not far to seek. The chick embryo is provided with an enormous quantity of yolk which cannot be made use of without a system of transportation, which conveys the yolk to the embryo. This system is the vascular system, and the heart is the pump which provides the mechanical energy for the transportation. In the frog, on the other hand, the yolk, which is present in much smaller quantity, is enclosed inside the embryo from the earliest stages of development, and there is no need for a precocious system of transportation.

The chick provides another example of acceleration in the precocious formation of the inner layer of cells (endoderm, yolk-epithelium) which precedes the appearance of a structure

known as the blastopore (primitive streak), instead of resulting from it as in the frog. In primitive mammals the amnion, extra-embryonic coelom, and allantoic mesoderm are formed after the embryo itself. But in man these structures precede the formation of the embryo, and show acceleration. Alternatively, this case may be regarded as one in which the human embryo is retarded relatively to its membranes.

Another example of acceleration may be obtained from a consideration of the tubes which grow out from the middle layer of cells of an animal (mesoderm) and place the space of the body-cavity (coelomic cavity) in communication with the exterior. These tubes are called coelomoducts, and Goodrich has emphasized that originally they served to free the reproductive cells which are formed in the body-cavity. As the reproductive cells are not freed until they are ripe, and they are not ripe until the animal is adult and has completed its development, the coelomoducts must originally have been formed in the last stages of ontogeny, as indeed they are in many worms. In other animals, however, and especially in the chordates, the coelomoducts make their appearance in the early stages of development, long before the reproductive cells are ripe, or even formed. In such animals, then, the formation of the coelomoducts has been accelerated, and the precocity of their appearance has made it possible for them to take on another function, viz. excretion or the getting rid of waste products. This function of excretion must be served from the earliest stages of development, and in those forms in which the coelomoducts only appear late, it is served by a different system of tubes altogether (the nephridia), which arise from the outer layer of cells. This latter system of tubes is, in general, not formed in the animals in which the coelomoducts arise in early stages of development.



FIG. 17. Hypermorphosis and acceleration in the lineage of *Gryphaea incurva*, 4. 1, *Ostraea irregularis*; 2, *Gryphaea dumortieri*; 3, *Gryphaea obliquata*. Attached area shaded. (From A. E. Trueman, *Geol. Mag.* 59, 1922.)

According to Osborn, horns were present only in the late stages of development in the early members of the titanotheres, whereas, in the later evolved members of this family, the horns were present before birth. This case has already been alluded to in Chapter IV, where the principle of allometric growth was mentioned. It was shown that the greater size of the allometric organ, and, consequently, the more rapid rate of action of the internal factors controlling it, were associated with an increase in the size of the body. It would seem, then, that in the case of the titanotheres the accelerated rate of action of the factors causes the allometric organ to arise earlier in ontogeny, just as in the case of the eye of *Gammarus* the stronger the factor the earlier the eye becomes black. Mehnert has indeed drawn attention to the fact that progressive structures, i.e. those which have become enlarged during phylogeny, tend to appear at earlier stages of ontogeny and to develop faster than they did in ancestral forms.

These examples show that it is just as possible for characters which appeared late in the ontogeny of the ancestor to undergo heterochrony and to appear early in the ontogeny of the descendant as vice versa. In these cases, the young stages of the descendant show greater similarity with the old stages than with the young stages of the ancestor in respect of the character in question. But the acceleration of these characters does not justify the conclusion that the early stages in the ontogeny of the descendant represent in miniature the complete adult ancestor. We cannot claim to obtain information as to the form of the adult in an ancestor from a study of the young stages in the development of a descendant unless acceleration has occurred, and, as we have seen, it may be that a few characters here and there are accelerated, but that is all.

It may be pointed out that those who believe in Haeckel's theory of recapitulation are accustomed to treat the repetition of the early ontogenetic stages of the ancestor in the early ontogenetic stages of the descendant as if these repeated stages represented an adult ancestor. They would, therefore, include in this chapter all the examples which we have used to illustrate progressive deviation. It may be recalled that we were in some cases able actually to show that the early stages of a descendant did not bear as great a resemblance to the adult as to the early

ontogenetic stages of the ancestor. There are also many cases in which our knowledge is insufficient to decide whether we have to do with deviation or acceleration. For example, starfish pass through a stage in which the larva becomes attached to its substratum and presents an appearance similar in form to that of the adult *Aristocystis*.

But until we know what the young *Aristocystis* was like, no conclusions can be drawn from this case.

Many recapitulationists would also be disposed to ascribe the resemblance between young descendant and adult ancestor (which admittedly can occur, as shown by the examples given in this chapter) to the 'inheritance of acquired characters'. We have already seen that this means the conversion of an external factor, which originally caused a modification in a character of the body, into an internal factor, which, being transmitted by inheritance, produces that same modification in the absence of that external factor. We may also repeat that satisfactory evidence as to the occurrence of this phenomenon is still required, and we may conclude this chapter with a description of cases which illustrate the care which is required in interpreting such evidence.

In mammals, teeth are formed beneath the gums and they may be cut before the young animal is born. Such teeth show unworn conical cusps or ridges, and it is only after birth that these cusps or ridges are worn down to flat surfaces in the molars, as a result of the wear and tear of grinding. Kükenthal discovered that in the early unborn embryo of the dugong the grinding teeth have unworn cusps, as one would expect. But in a later embryo, still unborn, he found that the teeth showed flat surfaces, as if they had been worn down by friction. Here, then, is a case in which the young animal presents a feature

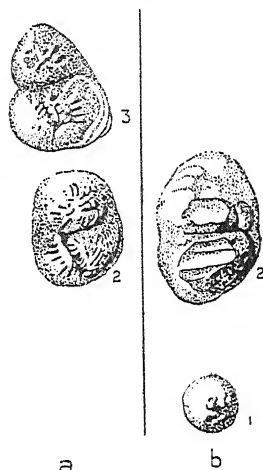


FIG. 18. View of the crowns of the upper molars of embryos of the dugong. In the younger embryo (*a*, 42 mm. long) the cusps are conical, while in the later embryo (*b*, 62 mm. long) flat surfaces are present, as if they had been formed by wearing down. (From Kükenthal.)

which is definitely characteristic of the effects of use in adult animals; the embryo 'recapitulates' the ground surfaces of the teeth of its adult ancestors. An effect has been produced in the absence of the external cause which normally produces it, for Kükenthal showed that even if the embryo had the habit of 'grinding its teeth' before it was born, they would not wear one another down for the teeth of the opposite jaws do not yet touch. How, then, are these flat surfaces produced? The teeth of the dugong are peculiar in that they are penetrated by canals through which blood-vessels pass, and it appears that the flat surfaces are due to removal of the tooth-substance by living cells, which were brought and are nourished by these blood-vessels. It is obvious that the internal factor which controls the formation of the flat surfaces in the unborn embryo is totally different from the external factor (friction) which produces the same result in the adult. Can any one suppose that friction in the adult has had anything to do with the origin of the internal factor which controls the resorption of the tooth in the unborn embryo? To accept such a conclusion would be to fall into the trap of the 'post hoc, ergo propter hoc' type of argument.

It is interesting to compare this case with that of the callosities of the ostrich. Duerden has shown that when the young ostrich hatches, it possesses a number of callosities already developed. These callosities are situated on the breast, the pubic region, and on each ankle-joint. Now, the callosities on the breast and pubic region are functional, for the ostrich rests its body on them when it crouches. But the callosities on the ankle-joints are not used, for the legs tilt inwards and so the callosities do not bear on the ground. Instead, the weight of the body 'rests upon an adjacent inner projection of the ankle, and the skin and scales here gradually thicken and form an accessory pad'.

The interest of this case lies in the following facts. All these callosities are 'inherited', i.e. internal factors controlling their formation are transmitted, but whereas in some (the accessory pads) this formation is evoked by external factors after hatching in each generation, in the others (breast, pubic, and ankle-joint callosities) these particular external factors are not required, for the formation takes place before hatching. But this is no

evidence for the assertion that the internal factors which control the development of the latter type of callosity are the result of the action of the external factors (friction and pressure) on the body of the ancestor, and we have no more information as to how the internal factors arose in this case than in that of the teeth of the dugong.

XIV

PAEDOMORPHOSIS AND GERONTOMORPHOSIS

THE result of the last few chapters has been to show that each of the theoretically possible effects of heterochrony in producing phylogeny has actually occurred in the evolution of different animals. Not only that, but the different characters of one and the same organism may have evolved by different modes. Thus in Graptolites, thecal elaboration shows neoteny, changes in direction of growth show acceleration; in the horse, skull dimensions show hypermorphosis, splint-bones show caenogenesis. The evolution of the hinge of *Gryphaea* shows combined hypermorphosis and acceleration. The following conclusions may therefore be drawn:

1. Qualitative evolutionary novelties can and do appear at all stages in ontogeny, and not solely in the adult.
2. Characters can and do change the time and order of their appearance in the ontogeny of the descendant as compared with that of the ancestor.
3. Quantitative differences between characters, resulting in heterochrony, play a part in phylogeny in addition to the introduction of qualitative novelties.
4. The different characters of an organism do not necessarily all evolve by the same mode.

It is to be noted that these conclusions remain equally sound whether the inherited factors which control the characters are regarded as Mendelian, or of any other nature whatsoever.

It now becomes necessary to consider the magnitudes of the phylogenetic effects which are associated with the different types of heterochrony; the magnitude being estimated by the value of the classificatory groups which contain the forms in question. This is by no means easy, as it is in many cases impossible to assess the phylogenetic effect of changes in a small number of characters of an organism.

It is difficult to estimate the value of the phylogenetic effect produced by some cases of acceleration, such as that of the

Associated with	The degree of divergence in Phylogeny between the following:	Is of the value of a
Caenogenesis	<i>Lineus gesserensis</i> , larval dimorphism	race
	<i>Chironomus salinarius</i> , „ „	race
	<i>Peripatus capensis</i> & <i>P. balfouri</i>	species
	<i>Acronycta tridens</i> & <i>A. psi</i>	species
	<i>Culex</i> , <i>Chironomus</i> & <i>Corethra</i>	genus
	<i>Unio</i> & other Lamellibranchs	family
	<i>Sitaris</i> & other Coleoptera	family
	<i>Haemocera</i> & other Copepoda	family
	Amniota & other Chordata	class
	<i>Portunion</i> & other Isopoda	family
Deviation	<i>Entoconcha</i> & other Gastropoda	family
	Hermit crab & other Crustacea	family
	Flat-fish & other Teleostei	order
	<i>Antedon</i> & other Echinodermata	order
	Gastropoda & other Mollusca	order
Neoteny	<i>Amblystoma</i> & axolotl	species
	<i>Polystomum integerrimum</i> & <i>P. ocellatum</i>	species
	<i>Homo</i> & other Primates	family
	Appendicularia & other Tunicata	order
	Proparia & other Trilobita	order
	Insecta & Myriapoda	class
	Chordata & Echinodermata	phylum
Adult variation	mutants	race or species
Hypermorphosis	<i>Gryphaea</i> & <i>Ostrea</i>	genus
	<i>Belone</i> & <i>Exocoetus</i>	genus
	<i>Achtheres</i> & other Copepoda	family
Acceleration	<i>Zaphrentis delanovei</i> & <i>Z. parallela</i>	species
	<i>Titanotherium</i> with & without horns	genus
	<i>Cycloclypeus</i> & <i>Heterostegina</i>	genus
	<i>Leptoplastus</i> & <i>Ctenophye</i>	genus

Characters rendered vestigial (i) by reduction are associated with deviation, (ii) by retardation are associated with neoteny.

heart in the chick, or of the coelomoducts in the chordates. The effect on phylogeny would seem to be very indirect.

The problem of the time in ontogeny of the appearance of characters distinguishing different groups offers a very fruitful field for research, in which a start has been made by Haecker in his studies on 'phenogenetics'. It is, however, desirable that these studies be continued in cases where the differences between the types are known to be controlled by genes, and in cases where the taxonomic or systematic relations are well established. Meanwhile, the table given above has no pretensions

to completeness, being composed merely of a few examples selected at random. On considering it, however, it does appear that the largest phylogenetic effects are produced in association with caenogenesis, deviation, and neoteny, which are to be regarded as having played a part in the evolution of Amniota, Gastropoda, Insects, and Chordates. Caenogenesis, deviation, and neoteny, of course, also produce small phylogenetic changes, as do adult variation, hypermorphosis, and acceleration. But it seems that a big change in evolution is more likely to occur if ancestral youthful characters become those of adult descendants, than if ancestral adult characters become youthful characters of the descendants. This correlation between early ontogenetic appearance of the evolutionary novelty and possible systematic importance of the resulting new type has also been recognized by Schindewolf.

Caenogenesis, deviation, and neoteny may then be grouped together since they are concerned with characters which appear early in the ontogeny, and they may be contrasted with adult variation, hypermorphosis, and acceleration, which are concerned with characters which appear late in ontogeny. The production of phylogenetic change by the introduction into the adult descendant of characters which were youthful (caenogenetic) in the ancestor, by means of deviation and neoteny, may be termed *paedomorphosis*. Phylogenetic change as a result of modification of characters which were already adult, by means of adult variation, hypermorphosis, and acceleration, may be termed *gerontomorphosis*.

A position in many respects similar to this has been arrived at by Sewertzow who distinguishes between evolution along broad lines, termed by him 'aromorphosis', and evolution of small details, 'idio-adaptation'. The former has been responsible for large changes, such as the production of the chordate brain, heart, jaws, and appendages. These are all innovations which do not restrict the possible habitats in which the organisms may live. On the other hand, idio-adaptation has restricted the modes of life of organisms by introducing specializations which fit them for some habitats and disqualify them from others. Such evolution has produced rays and skates, flat-fish, snakes, flightless birds, and countless other highly adapted forms. Sewertzow's terms aromorphosis and idio-adaptation

are therefore in some measure the ecological equivalents of our paedomorphosis and gerontomorphosis, but with stress layed on the importance of the evolutionary novelty rather than on the stage in ontogeny at which it appeared. The latter aspect of the problem is covered by Sewertzow's terms 'archallaxis', 'deviation', and 'anaboly', for the appearance of novelties at early, middle, or late stages of development. Major novelties are likely to result from 'archallaxis', while 'anaboly' leads to modification and specialization of structures already present.

It may be noted that Sewertzow's 'idio-adaptation' is practically the equivalent of Osborn's 'adaptive radiation'.

If it be true that big evolutionary changes, and therefore the large groups of the animal kingdom, are due to paedomorphosis, it should be possible to correlate the characteristics of large groups with the essential feature of paedomorphosis, viz. the appearance of characters in early stages of the ontogeny of the ancestor. Now, the large groups of the animal kingdom such as phyla and classes have two characteristics. In the first place, the animals in any phylum or class differ considerably from animals in other phyla or classes, i.e. there has been considerable phylogenetic structural change between the different phyla and classes. Next, the large groups, phyla or classes, contain more numerous different types within them than do the smaller groups such as families, genera, or species. This means that the changes which gave rise to the large groups have enabled the animals in these groups to go on evolving further and in more numerous directions than the animals in the small groups. The potentiality of evolving further is called *phylogenetic* or *evolutionary plasticity*, and so it becomes necessary to show that paedomorphosis is capable of producing large changes in phylogeny without sacrificing plasticity, and that gerontomorphosis is not capable of this.

First, as to the amount of structural change effected, we know that the adult form is the result of ontogeny, and also that the earlier a character appears in ontogeny, the longer it has to proceed with its development. Experiments on the gipsy moth have proved that the earlier the male characters appear in would-be females, the greater is the change that results in the adult form, viz. intersexuality. That the degree of divergence should be greater the earlier the divergence sets in, is only

another way of expressing von Baer's law of the greater resemblance between young forms, and we have seen that in phylogeny this has been brought about by deviation. On the other hand, characters which appear late in ontogeny have not much time as a rule to produce much effect before development ceases. The large amount of structural change effected in evolution by paedomorphosis is therefore based on the principle of deviation, as is illustrated by the supposed evolution of the whole class Gastropoda as a result of a variation in the young.

Deviation and neoteny combined may also play a part in producing large structural changes. In animals in which the young stages have to undergo considerable change before the adult form is reached, a retention of the form of the young stage will produce a phylogenetic change as big as (but in opposite direction to) the difference between young and adult. This is illustrated by the supposed evolution of chordates from forms like larval Echinoderms. The adult chordate differs as much from the adult Echinoderm as the latter does from the larval Echinoderm.

The question as to the part which neoteny or deviation may be expected to have played in the retention or increase of evolutionary plasticity is very difficult to answer, largely because of the lack of direct evidence bearing upon it. A difficulty also arises from the fact that the term 'plasticity' has been used in many different senses.

Genetic plasticity is the ability of individuals of a species to show a high degree of variance, and this condition obtains when the number of individuals carrying genes in the heterozygous condition, and the number of those genes, is large. In such species the possibilities of recombination of genes are numerous, and there is a reserve of recessive genes which may come into play, in one way or another, in the new conditions which recombinations and permutations provide.

A species undergoing paedomorphosis will find itself in possession of a number of genes whose functions were to control characters which no longer appear, since the old adult characters will be lost in neoteny, and old structures will be replaced by new ones in deviation. It is, therefore, possible to imagine that these 'unemployed' genes are available for new variation,

and that paedomorphosis may contribute directly to an increase of genetic and evolutionary plasticity in this way.

Yet another sense in which the term plasticity has been used relates to the ability of a tissue to undergo further or other differentiations. This is *histogenetic plasticity*. Experiments on regeneration and tissue-culture have shown that there exists an antagonism between the degree of specialization of a tissue and its power to grow and become specialized in other directions. At the outset of ontogeny, all the cells to which the fertilized egg has given rise are more or less similar, and devoid of any specialization or differentiation. Such cells are described as being in the *embryonic* or undifferentiated condition. Experiments have shown that embryonic cells are capable of rapid growth, and that their eventual fate is not yet irrevocably determined. A cell which would normally have undergone specialization to form part of the skin for instance, can be made to turn into part of muscle, or stomach, or nervous system, as Mangold has shown. As development proceeds, however, the cells and tissues become irreversibly committed to specialization and differentiation, each along its own line, and can no longer alter their prospective fate. In other words, the histogenetic plasticity of the tissues which characterizes the young stages of development is lost at the older stages. Now, since phylogeny is the result of changes in successive ontogenies, it is impossible to expect much alteration to take place when the animal has reached the later stages of its development. This is presumably why gerontomorphosis can only result in the production of small groups of animals, which become more and more specialized and incapable of evolving further. But paedomorphosis is concerned with the young stages of development, and the question arises whether, if the more or less embryonic condition of the tissues at these young stages can be preserved into later stages, these tissues will still be capable of undergoing a considerable degree of further alteration. The question is whether prolonged histogenetic plasticity could play any part in increasing genetic and evolutionary plasticity. In the absence of evidence on the genetic control of the processes of histogenesis and determination in early development, this is very difficult to answer, and had better be left.

It is to be noted that caenogenesis may also give rise to

highly specialized products in the way of youthful forms, but these will also have lost their plasticity; and as it is unlikely that their characters will ever become adult characters, the question of their effects on phylogeny by means of paedomorphosis does not arise.

It appears, then, that by paedomorphosis evolutionary novelities may give rise to characters conferring on their owners a distinctness of high systematic importance. For instance, ordinal characters may precede those of familial or generic value in phylogeny. In this connexion Matthew's studies on eocene mammals are of great interest. In the basal Eocene, the Perissodactyla, Artiodactyla, Rodentia, and Lemuroidea are all represented by simple forms, ordinally distinct but not yet differentiated into families. In other words, 'large' evolution had produced the orders; 'small' evolution had not yet split them up. In this connexion, it is interesting to note that Kölliker envisaged the possibility of 'large' evolution by large, fairly rapid changes, and based his view on the fact that in the phenomenon of alternation of generations, forms can give rise to others which are structurally different. The hydroid polyp, for instance, produces the medusa.

We may conclude, then, that evolution by gerontomorphosis produces relatively small changes which sacrifice the power of changing further, and that, on the other hand, paedomorphosis produces large changes which do not sacrifice that power. If gerontomorphosis were the only possible method of evolution, as Haeckel's theory of recapitulation would suggest, phylogeny would gradually slow down and become stationary. The race would not be able to evolve any further, and would be in a condition to which the term 'racial senescence' has been applied. It would be difficult to see how evolution was able to produce as much phylogenetic change in the animal kingdom as it has, and it would lead to the dismal conclusion that the evolutionary clock is running down. In fact, such a state of affairs would present a dilemma analogous to that which follows from the view that in the universe energy is always degraded. If this were true, we should have to conclude that the universe had been wound up once and that its store of free energy was irremediably becoming exhausted. We do not know how energy is built up again in the physical universe; but the analogous

process in the domain of organic evolution would seem to be paedomorphosis. A race may become rejuvenated by pushing the adult stage of its individuals off from the end of their ontogenies, and such a race may then radiate out in all directions by specializing any of the stages in the ontogenies of its individuals until racial senescence due to gerontomorphosis sets in again. It is, however, to be noted that if a race has become excessively over-specialized, even the younger stages of the ontogenies of its individuals may have lost their plasticity. In this way, excessive adaptation may prevent the possibility of paedomorphosis.

When Conklin writes that 'in every well-tried path of evolution progress has practically come to an end', he expresses the results of gerontomorphosis. And if we look round to try to see which of the species of animals living to-day are the ancestors of the leading evolutionary novelties of say ten million years hence, focusing our attention only on adult forms we find it impossible to point out any such ancestor. If any new orders, classes, or phyla of animals are to arise by evolution in the future, it is to the early stages of animals alive to-day that we must look for their characterizations. In this connexion, a remark by Haldane is of great interest: 'If human evolution is to continue along the same lines as in the past, it will probably involve a still greater prolongation of childhood and retardation of maturity. Some of the characters distinguishing adult man will be lost. It was not an embryologist or palaeontologist who said, "Except ye . . . become as little children, ye shall not enter into the kingdom of heaven".' Not only physical characters but types of behaviour and mental traits may be susceptible of paedomorphosis and gerontomorphosis.

We may, then, picture the evolution of a race as a series of revolutions; periods of gerontomorphosis alternating with bouts of paedomorphosis. Such a possibility has also been envisaged by Sewertzow, who imagines an alternation between periods of 'aromorphosis' and of 'idio-adaptation' (see p. 80), by Wedekind, and by Beurlen who accept the view that bouts of 'large' and of 'small' evolution have alternated.

The terms gerontomorphosis and paedomorphosis, therefore, express not only the stage in the life-history of an animal with which they are concerned, but they also convey the meaning

of racial senescence and rejuvenescence. It is interesting to note that as a result of considerations based on a different line of thought, Child has been led to express similar views. 'If evolution is in some degree a secular differentiation and senescence of protoplasm, the possibility of evolutionary rejuvenescence must not be overlooked. Perhaps the relatively rapid rise and increase of certain forms here and there in the course of evolution may be the expression of changes of this sort.'

The concept of paedomorphosis renders another service to the study of phylogeny. If two animals in a phylogenetic series are compared as regards their adult structure, one animal may be regarded as antecedent to the other in that it either does not possess, or possesses only partially developed, a character which the other animal possesses fully developed; or, it still possesses a structure which the other animal has lost. The antecedent animal in such a case is called *primitive*, and the other, *specialized* or *secondary*. These words can only be used to describe members of a phylogenetic series, and one member in terms of another, for an animal which is primitive in respect of one may be specialized in respect of another animal. For instance, a reptile is more primitive than a mammal because the reptile's heart has only three chambers to the mammals' four. But a reptile is more specialized than a fish, because the heart of the latter has only two chambers.

Now, it is often said that the structural changes which take place in evolution are irreversible, and that no case is known in which a race of animals after having lost a character acquires that *identical* character again. The problem is, however, not quite so simple, for the 'loss' of a character may be due to fairly recent changes in the hereditary factors, changes which may still be reversed resulting in a reconstitution of the original conditions. Or the loss of a character may be due to long-standing hereditary changes incapable of being reversed. Guinea pigs have lost the thumb and the little toe; dogs have lost the big toe. But these digits can be redeveloped under certain genetic conditions, as Stockard has shown. By particular recombinations of genes, the original conditions are reconstituted under which all the digits are developed. It looks as if the 'loss' of the digits was due to the acquisition of genes and genetic conditions resulting

in their suppression. The phylogenetic history of the horses has involved the reduction and loss of all fingers and toes except the third. In some very exceptional cases horses may have extra fingers or toes besides the third. Here it is unlikely that the original ancestral conditions are exactly reproduced; for some unknown reason the rudiments of the extra digits grow large instead of being reduced to vestiges. But whatever the cause, the result is the redevelopment of lost structures. However, it is impossible to imagine that any descendants of the horses may reacquire all five fingers and toes and evolve further on those lines. The horses are committed to their phylogenetic line and cannot reacquire all the genetic factors which they have lost. As Dollo has put it, the past is indestructible. But while a character once lost is lost for ever if the genetic factors and conditions controlling its formation are irretrievably lost or irrevocably changed, a substitute character may appear which fulfils the same function as the old character, but is always structurally distinct and easily recognizable. As an example we may take the tendency which is observable in the phylogeny of the colonial hydroids for the originally free-swimming medusa to become more and more reduced to the condition of a sac which never becomes detached and therefore has lost its freedom. In some cases, however (e.g. in *Dicoryne*), such a sac may become detached and regain its mobility, but it cannot be mistaken for a medusa. The muscles which served for the locomotion of the medusa have gone and are not replaced, and for its locomotion the sac has to have recourse to a different system altogether, viz. cilia. Thus, while structural reversibility appears never to have taken place in evolution, functional return to a previous condition, using other instruments, is not uncommon.

The result of these considerations is to show that it is not possible to derive one form in phylogeny from another if the latter is too specialized. Crow has expressed this in the following words: 'As one higher class succeeds another, so the higher members of the lower class may disappear, the lower ones remaining. It is from the latter alone, the more undifferentiated species of the older class, that the new class type can arise.' But the reason why these lower or primitive members of the class were more undifferentiated is simply that they have

retained the plasticity which their previous paedomorphosis gave them, and have not undergone extensive gerontomorphosis, or that they have reacquired plasticity by a fresh bout of paedomorphosis, if the previous gerontomorphosis was not too excessive. For the same reason, highly specialized products of caenogenesis cannot be expected to contribute material to be acted upon by paedomorphosis.

It is probable that natural selection was not inactive in favouring the evolution of groups by paedomorphosis. The results of gerontomorphosis are progressive specialization of the adult structure, usually in adaptation to some more or less restricted mode of life. Such adaptation entails either the development or loss of characters which handicap the animal in any walk of life other than its own. If, then, climatic or other external factors arise or change, upsetting this mode of life, the animal being unable to evolve further will have no alternative to extinction. But primitive animals are not committed to any particularly restricted mode of life; they are generalized instead of being specialized, and they will be less likely to undergo extinction as a result of environmental change, for they possess plasticity. And we have just seen that the primitive nature of an animal is associated with the plasticity which we believe is the result of paedomorphosis.

It is worth noticing that man, whose phylogeny we have seen to be characterized by paedomorphosis, largely owes his success to the fact that he is not adapted to any particularly restricted mode of life at all. Instead, he is fitted for all sorts of habits, climates, and circumstances. Man himself is generalized, not specialized, and, as Elliot Smith and Wood Jones have emphasized, his body has retained a large number of primitive features which other mammals have lost.

A word may be said in connexion with the bearing of paedomorphosis on the construction of phylogenetic trees or pedigrees. We have seen (p. 80) that characters conferring important systematic distinction are more likely to arise by means of paedomorphosis than gerontomorphosis. We have also seen that early phylogenetic stages are called primitive, late ones specialized or secondary. We may call the early ontogenetic stages (embryonic or larval) young, and the late ones adult. Now, if the theory of recapitulation were of universal applica-

tion, it would follow that an animal which in its adult stage possesses characters which are present only in the young stages of development in other animals, would always be regarded as phylogenetically primitive. But this would lead to absurd conclusions, as, for instance, that the human stock gave rise to apes, that the so-called flightless birds gave rise to flying birds, or that the neotenous *Urodeles* gave rise to the other newts, instead of vice versa.

The possession of embryonic or larval characters in the adult does not necessarily prove that the possessor is primitive, for it is equally if not more likely to be due to neoteny, and therefore to be phylogenetically secondary. Lowe has revealed the most interesting fact that the plumage of the ostrich and of the penguin remains throughout life in the condition of the down plumage of the chicks of flying birds. Since the wings of the ostrich and other so-called flightless birds and of penguins must have been derived by degeneration from those of flying birds, it is to be concluded that these embryonic and larval features have been secondarily prolonged and retarded by neoteny in the evolution of flightless birds and penguins from flying birds.

Lastly, we may draw attention to a small but not unimportant point of terminology. For Haeckel, a caenogenetic character was necessarily originally youthful, a palingenetic character originally adult. But as the essential feature of Haeckel's palingenetic characters was that they were ancestral, and as we have seen that ancestral characters may originally have been adult or youthful, it is best to discard the term palingenetic in favour of Garstang's term palaeomorphpic. A palaeomorphpic character may of course have been originally caenogenetic, i.e. have made its first appearance in early stages of ontogeny. Conversely, characters of more recent origin, to which Garstang applies the term neomorphpic, may have originated in terminal ontogenetic or adult stages.

XV REPETITION

WE have now come nearly to the end of our review of the relations which ontogeny and phylogeny bear to one another, and we have seen that the characters which appeared in the ontogeny of the ancestor tend to reappear in the ontogeny of the descendant, either at a corresponding stage of development, or earlier, or later. We have also seen that the accelerated appearance of a character in the ontogeny of a descendant cannot be construed as the pressing back of a complete adult ancestral stage into earlier stages of development, especially as, accompanying the acceleration of some characters, there may be neoteny of others (cf. Graptolites, horses). There is, then, no recapitulation in the Haeckelian sense of accelerated repetition of adult stages. But there *is* repetition, or palaeogenesis. Characters which appeared in the ancestor do tend to appear in the descendant, and, whatever stage these characters may 'represent', it is difficult to avoid the impression that the enthusiasm of the recapitulationists is really based on this obvious fact of repetition. If only the recapitulationists would abandon the assertion that that which is repeated is always the *adult* condition of the ancestor, there would be no reason to disagree with them. We have seen that that which is repeated in the ontogeny of the descendant may represent the embryonic or larval just as well as the adult characters of the ancestor, and that the retarded repetition of youthful ancestral stages is of particular importance because of the part which it plays in pedomorphosis. The appearance of characters in the early stages of development is caenogenesis, and these characters which loom so largely in neoteny and deviation are flies in the Haeckelian ointment of recapitulation, for his theory was bound to treat them as exceptions to his rule of evolution. It is because these early developed characters are not exceptions in phylogeny, together with the fact that phylogeny is the result of ontogeny instead of being its cause, that we reject Haeckel's theory of recapitulation.

We are left with heterochrony, or variations in time of the

repetition of characters in successive ontogenies, and the question which at last arises is, why are characters repeated?

A word of caution is necessary here. Repetition of characters interests us as a reflection of events which were manifested in the ontogenies of the ancestors and are continued in those of the descendants. But there are cases of repetition which clearly call for a special explanation. For instance, Needham has drawn attention to the fact that the nitrogen excreted by adult invertebrates, fishes, and birds takes the form of ammonia, urea, and uric acid respectively. The chick embryo starts by excreting ammonia, then urea, and lastly uric acid, thus apparently providing a case of recapitulatory repetition of adult ancestral characters. But apart from the fact that the chemistry of urea-production in the chick embryo is not the same as that of adult fishes, this case is instructive in bringing out the principle of parallelism of processes showing increasing degrees of complexity, exemplified by the series ammonia-urea-uric acid. Many other such sequences are cited by Needham, and there is apparently a natural order in which things can be done: a necessitation which affects all ontogenies alike. Repetition of such sequences is evidence, therefore, not of any influence of phylogeny on ontogeny, but of the limitations of physico-chemical possibilities in the transition from the simple to the more complex.

Attention may now be turned to the repetition of vestigial structures. Why does the snake embryo repeat the development of its pharyngeal pouches and not that of its limbs? One answer to this question has been given by Needham: the structures whose development is repeated are in some way or other essential. The fact that the pharyngeal pouches of an amniote embryo will never become gill-slits is no evidence that these pouches are useless. On the contrary, they play an essential part in providing the rudiments of a host of structures, e.g. tympanic cavity, tonsils, thymus and parathyroid glands. In fact, we are here invoking Kleinenberg's principle of substitution: the ontogenetic development of an evolutionary novelty is dependent in some way on the presence of the old structure for which the novelty is substituted. The notochord may perhaps be 'necessary' for the development of the vertebrae that replace it, though this has not been proved by direct experiment.

On the other hand, the result of the experiments of Spemann and his school have revealed the indispensable nature of the notochord and shown that embryonic 'necessities', now known as 'organizers', are plentiful. It is therefore not surprising that the development of such 'organizers' should be repeated in every ontogeny, even if such rudiments no longer give rise to the same structures as in the ancestors, or, indeed, to any structures at all. The functional significance of the repetition of structures has also been stressed by Lehmann.

Another answer to the question, why are characters repeated? is so simple that it and its implications have often been overlooked. It has been most aptly formulated by Morgan and by Broman. Characters are repeated when the groups of factors or genes which controlled their appearance in the ancestors have been transmitted to the descendants, and the appropriate environmental conditions persist. Repetition is, therefore, evidence of *affinity* between ancestor and descendant, which might not always be obvious by a comparison between the structures of the adult forms, and this is the real value of embryology in the interpretation of evolution. Given the possibility of heterochrony, it is idle to assume that the repeated character represents an ancestral adult rather than an ancestral youthful condition, and therefore any attempt to reconstruct the ancestral adult structure from the embryonic or larval structure of the descendant must be unsound. All that can be said is that since the ancestor gave rise to the descendant, it must have been primitive, and primitive animals are less specialized. Therefore, it is probable that the ancestral adult form did not depart as much from the ancestral youthful form as the adult form of the descendant departs from its youthful form. Thus the ancestral adult structure can only be inferred and not proved from a study of embryology.

The nature of the repetition of characters in successive ontogenies throws an interesting light on the phenomena which are usually included under the term atavism. In the horse, all the fingers and toes have been lost except the third on each limb. When, as very occasionally happens, a horse has an extra finger or toe in addition to the third, it presents a certain resemblance to a more primitive phylogenetic condition in which the reduction of fingers and toes had not proceeded as far as they have in

the normal structure of the modern horse. But does this mean that the abnormal horse with extra fingers has 'gone back' to an ancestral type? Gegenbaur showed some time ago that this could not be affirmed, and indeed each case must be considered on its merits. In some cases there can be no question of atavism, for the extra digit is merely a product of the subdivision of the originally undivided rudiment. Thus a horse may have a subdivided third digit, which is not at all the same thing as having a third and fourth digit. In other cases, as in those of the guinea-pigs and dog mentioned in the previous chapter, an ancestral condition is reproduced. As Stockard has shown, these atavistic phenomena must be regarded as due to the reconstitution of the original genetic conditions, by suitable recombinations of genes.

In the more primitive insects such as *Iapyx* or *Machilis* the reproductive organs are repeated in each of seven segments of the abdomen. That this is a primitive feature cannot be doubted, for the essence of the segmentation of the body is the repetition of the reproductive glands, as in many worms. In the higher insects, of which the gipsy moth is an example, the reproductive glands are localized in one abdominal segment only and are not repeated. Goldschmidt has found, in the course of experimental breeding of races which differ in the relative speeds of development, that gipsy moths can be obtained in which the reproductive glands are segmentally repeated. This condition is to be explained by the different rates of actions of the factors which control the processes of segmentation and of formation of the reproductive glands, respectively. Normally, the latter are quick enough to form the reproductive gland before the processes of segmentation can divide it up between several segments. But if these processes are relatively delayed, the processes of segmentation will effect a partitioning of the reproductive gland before the latter is definitely formed, and so 'reproduce' the ancestral condition. Atavism here is, therefore, due to the reproduction of a set of conditions (a definite system of reaction-speeds) which obtained in the ancestor.

To a case such as that just described, in which the formation of a structure is relatively delayed, Schulze's term *hysterotely* is applied. The converse condition known as *prothetely*, in which the development of a structure is relatively accelerated, has,

curiously enough, also provided cases which have been regarded as atavistic. For instance, the occasional presence of wings in caterpillars has been held to reflect a primitive ancestral condition of insects in which development is progressive and gradual without the abrupt metamorphosis which characterizes the higher forms. But here again, Goldschmidt has shown that the condition is merely the result of changes in the rates of activity of different processes, and has no phylogenetic significance at all.

Analogous results of an atavistic nature have been obtained by Runnström in the course of his investigations of experimental embryology of Echinoderms. The larvae of Echinoderms are characterized generally by the possession of three pairs of body-cavities, but in the larva of *Antedon* the first and second cavities on the right side are normally not formed. If, however, a larva of *Antedon* is cut into two by a transverse cut, the posterior half develops these cavities, thereby differing from a normal *Antedon* larva and resembling the larvae of other Echinoderms. This case of atavism is to be explained by the re-establishment of an ancestral set of conditions brought about by the removal of an inhibiting factor which was eliminated when the anterior half of the larva was cut off. A number of other atavistic appearances can be produced in the same way.

Lastly, we may consider some atavistic phenomena in man. It was shown in Chapter VIII that the evolution of man was in a large measure due to neoteny and retardation, and we saw in Chapter III that the rate of development in mammals is under the control of the ductless glands which secrete hormones. During human phylogeny, therefore, the rate of development of the body must have been progressively retarded by the action of the ductless glands. Suppose now that, for some pathological reason, one or other of the ductless glands ceases to exert this retarding function, the result will be the production of a man with so-called pithecoïd characters: the hair will be over-developed, or the skin dark, or the brow-ridges accentuated, or the jaws larger, or the length of the bones will be increased, or sexuality will be precocious, or the sutures between the bones of the skull will close up prematurely. These features are atavistic in that they result from a reversion to the set of circumstances under which development took place in the ancestor.

Atavism is, therefore, based on an inheritance of similar genetic factors by the descendant from the ancestor, and the reconstitution of similar conditions. But, like normal development, atavism is actually brought about by that new creation of an animal, which constitutes ontogeny. The atavistic feature is not directly inherited from the ancestor as such, for nothing is solely inherited without also being acquired.

The opposite condition to repetition or palaeogenesis is seen in those cases in which the primitive processes of development of a character in an ancestor have been discarded in the descendant, and replaced by modified processes which Garstang has termed neogenetic. Neogenesis will be the result of caenogenetic modifications of development, such as those mentioned on page 34. It is important to note that the terms palaeogenetic and neogenetic refer to processes of development, old and recapitulatory or new and anti-recapitulatory, respectively. On the other hand, the terms palaeomorphic and neomorphic denote the phylogenetic age of characters, regardless of the stage of ontogeny in which they originated in the ancestor, or of the manner in which they develop in the descendant.

XVI CONCLUSIONS

THE line of argument which forms the subject of this book may be summarized as follows:

Ontogeny is the result of the action of external factors in evoking responses from the internal factors of an animal to which the latter were transmitted by inheritance from its parents.

Phylogeny is provisionally to be regarded as a series of adult forms, which are disconnected and causally unrelated to one another, each adult form being the result of an ontogeny which differs from the previous one.

Successive ontogenies are related to one another by the transmission of internal factors from fertilized egg to fertilized egg.

Modifications in ontogeny (in a constant environment) are due to changes in the internal factors.

Phylogeny is therefore due to modified ontogeny.

Phylogeny plays no causal part in determining ontogeny.

The internal factors exert their effects at certain definite rates.

Modification of the rate of action of the internal factors in successive ontogenies will result in heterochrony.

Evolution is brought about by acquisition of qualitative novelties, and by the production of novel situations by quantitative alteration of the rate of action of the internal factors.

New characters may appear at all stages of ontogeny, and by heterochrony they may be retarded or accelerated, so as to appear later or earlier in subsequent ontogenies.

Characters present in the early stages of ontogeny have (provided that they are not too specialized) played an important part in evolution by paedomorphosis, resulting in large structural changes without loss of plasticity.

Characters present in the late stages of ontogeny have played an important part in evolution by gerontomorphosis, resulting in relatively small structural change with loss of plasticity.

Paedomorphosis and gerontomorphosis may act alternately in the phylogeny of a race, the former producing racial rejuvenescence, the latter racial senescence.

Recapitulation, i.e. the pressing back of adult ancestral stages

into early stages of development of descendants, does not take place, although there may be acceleration of one structure or another.

Repetition of ancestral ontogenetic stages in the ontogeny of the descendant, whether retarded or accelerated, is due to the transmission of internal factors from ancestor to descendant.

Similarity in ontogeny between any animals is a proof of their affinity, and no evidence as to the adult structure of the ancestor.

Atavism is due to the re-establishment in the ontogeny of the descendant of a set of circumstances which was present in the ontogeny of the ancestor.

It goes without saying that even if the views set forth here are correct, they do not provide an 'explanation' of evolution, for there remains the problem of how and why novelties arise, and why they show heterochrony in those cases in which they do. But it is claimed that after dethroning the theory of recapitulation we are able to make a better synthesis of our knowledge of embryology and evolution.

In the first place, we are able to consider possibilities other than the repetition of adult characters by youthful descendants, and, as we have seen, these possibilities are interesting and important. The relations of evolutionary plasticity to genetic plasticity encourage the hope that progress in knowledge of the latter, which is accessible to experimental investigation, will increase our knowledge of the former. And in both cases the variability which plasticity denotes will have to be studied from the embryological aspect.

In the second place, we are rid of a mental strait-jacket which has had lamentable effects on biological progress. It is no exaggeration to say that Haeckel's theory of recapitulation has thwarted and delayed the introduction of causal analytic methods into embryology. For instance, when His attempted to analyse ontogenetic processes into simpler components, such as growth, expansion, adhesions, perforation, &c., Haeckel ridiculed them on the grounds that 'each of these simple ontogenetic processes of unfolding is the result of an extremely complicated series of historical events. It is causally determined by the thousands of phylogenetic changes, by the innumerable hereditary and adaptive alterations, which the ancestors of the

organism in question have undergone during the course of millions of years'.

Clearly, if phylogeny was the mechanical cause of ontogeny as Haeckel proclaimed, there was little inducement to search for other causes. The crux of the matter, as J. S. Huxley has pointed out, is that it is essential to realize the difference between the descriptive historical and the causal analytic methods of study of living organisms.

And this leads us to a remarkable conclusion. The analytical and experimental study of embryology is providing an increasing body of information concerning the chains of linked causes the result of which is ontogenetic development. On the other hand, palaeontological studies are providing an increasingly precise description of the results of phylogenetic evolution. We may now ask ourselves the question, what is the nature of the assistance which each study can bring to the other?

Clearly, phylogeny does not explain ontogeny at all. Even if we had a *complete* phylogenetic series of adults ancestral to any given descendant, it would not help us to understand the processes of fertilization, cleavage, differentiation, organogeny, &c., which take place in the ontogeny of that descendant. The historical descriptive study of evolution has no bearing on the causal analytic study of embryology. To use an analogy suggested by Woodger, rockets go up on November 5th (a) because of an historical tradition in virtue of which this event is repeated each year on this day, (b) because the rockets contain charges of a substance, gunpowder, whose properties are to undergo combustive expansion resulting in the exertion of force on the rockets. The properties of gunpowder are not deducible from a study of the biography of Guido Fawkes. Nor are those of a fertilized egg from a study of the phylogenetic series of adults in the evolutionary history of its species.

Conversely, if we knew all the processes involved in the events of ontogeny, such knowledge would not of itself provide an explanation of phylogeny. For past phylogeny no method of study other than the historical descriptive is possible. But since phylogeny is but the result of modified ontogeny, there is the possibility of a causal analytic study of present evolution in an experimental study of the variability and genetics of ontogenetic processes.

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BIBLIOGRAPHY

- AGASSIZ, L. (1859). *An Essay on Classification*, p. 269, London, 1859.
- ALLIS, E. P. (1936). 'Comparison of the Latero-sensory lines', *Journal of Anatomy*, **70**, 293.
- ARISTOTLE, in SINGER, C. (1922). *Greek Biology and Greek Medicine*, p. 45. Oxford, 1922.
- BAER, K. E. VON (1828). 'Ueber Entwicklungsgeschichte der Thiere', *Beobachtung und Reflexion*. Königsberg, 1828.
- (1866) 'De la découverte de larves qui se propagent', *Bulletin de l'Académie Impériale des Sciences de St. Petersburg*, **9**, 64.
- BARCROFT, J. (1938). 'The Brain and its Environment'. Yale University Press.
- BATESON, W. (1913). *Problems of Genetics*, p. 67. Yale, 1913.
- BEECHER, C. E. (1893). 'Some Correlations of Phylogeny and Ontogeny in Brachiopoda', *American Naturalist*, **27**, 599.
- DE BEER, G. R. (1938). 'Embryology and Evolution'. In *Evolution: Essays presented to E. S. Goodrich*. Edited by G. R. de Beer. Oxford, 1938.
- BERG, L. (1926). *Nomogenesis or Evolution determined by Law*. London, 1926.
- BEURLEN, K. (1930). 'Vergleichende Stammesgeschichte', *Fortschritte der Geologie und Paläontologie*, **8**, 317.
- BOLK, L. (1926). *Das Problem der Menschwerdung*. Jena, 1926.
- BONNET, C. (1764). *Contemplation de la nature*. Amsterdam, 1764.
- BRINKMANN, R. (1929). 'Statistisch-biostratigraphische Untersuchungen an Mitteljurassischen Ammoniten über Artbegriff und Stammesentwicklung', *Abhandlungen der Gesellschaft der Wissenschaften zu Göttingen. Math.-Phys. Kl. N.F.* **13**.
- BROMAN, I. (1920). *Das sogenannte Biogenetische Grundgesetz*. München und Wiesbaden, 1920.
- BULMAN, O. M. B. (1933). 'Programme-evolution in the Graptolites', *Biological Reviews*, **8**, p. 311.
- BUTLER, P. M. (1937). 'Studies of the Mammalian Dentition', *Proceedings of the Zoological Society of London, B*, p. 103.
- BUXTON, L. H. D., & DE BEER, G. R. (1932) 'Neanderthal and Modern Man', *Nature*, **129**, 940.
- BUXTON, P. A. (1938). 'Anopheles and the Species Problem', *Proceedings of the Zoological Society of London, C*, p. 57.
- CASTLE, W. E., & GREGORY, P. W. (1931). 'The Embryological Basis of Size Inheritance in the Rabbit', *Journal of Morphology*, **48**, 81.
- CHAMPY, C. (1924). *Sexualité et hormones*. Paris, 1924.
- CHILD, C. M. (1915). *Senescence and Rejuvenescence*, p. 464. Chicago, 1915.
- (1924). *Physiological Foundations of Behavior*. New York, 1924.
- CONKLIN, E. G. (1922). *Heredity and Environment*. Princeton, 1922.
- COPE, E. D. (1868). 'On the origin of Genera', *Proceedings of the Academy of Natural Science, Philadelphia*, p. 242.

- COUPIN, F. (1925). 'Étude du cerveau du chimpanzé nouveau-né', *Bulletin de la Société d'Anthropologie de Paris*.
- COUSIN, G. (1938). 'La néoténie chez *Gryllus campestris*', *Bulletin biologique de France et de Belgique*, **72**, 79.
- CROW, W. B. (1926). 'Phylogeny and the Natural System', *Journal of Genetics*, **17**, 129.
- DARWIN, C. (1859). *The Origin of Species*, p. 611 (Edition: London, 1911).
- DETWILER, S. R. (1926). 'Experimental Studies on Morphogenesis in the Nervous System', *Quarterly Review of Biology*, **1**, 61.
- DEVAUX, E. (1933). *Trois problèmes: l'espèce, l'instinct, l'homme*. Paris, 1933.
- DIVER, C. (1939). 'Aspects of the Study of Variation in Snails', *Journal of Conchology*, **21**, 91.
- DOLLO, L. (1922). 'Les Céphalopodes déroulés et l'irréversibilité de l'évolution', *Bijdragen tot de Dierkunde*, **22**, 215.
- DROOGLEVER FORTUYN, A. B. (1922). 'Verklebung von Leberzellbalken in Säugetieren', *Bijdragen tot de Dierkunde*, **22**, 13.
- DUERDEN, J. E. (1924). 'Methods of Evolution', *Science Progress*, **18**, 560.
- EAL, N. B. (1931). 'The Development of the Mandible in the Elephant', *Proceedings of the Zoological Society of London*, 115.
- EMER, G. H. T. (1890). *Organic Evolution*. (English translation), London, 1890.
- EKMAN, G. (1930). 'Über Entwicklung und Vererbung', *Annalia Societatis Zoologicae-botanicae Fennicae*, **10**.
- ELLIOT SMITH, G. (1927). *Essays on the Evolution of Man*. Oxford, 1927.
- FENTON, C. L. (1931). 'Studies of Evolution in the genus *Spirifer*', *Publications of the Wagner Free Institute*, **2**, 8.
- FORD, E. B. (1928). 'The Inheritance of Dwarfing in *Gammarus chevreuxi*', *Journal of Genetics*, **20**, 93.
- FORD, E. B., & HUXLEY, J. S. (1927). 'Mendelian Genes and Rates of Development in *Gammarus chevreuxi*', *British Journal of Experimental Biology*, **5**, 112.
- FRANZ, V. (1927). 'Ontogenie und Phylogenie', *Abhandlungen zur Theorie der organischen Entwicklung*. Berlin, 1927.
- FUCHS, H. (1930). 'Beiträge zur Entwicklungsgeschichte und vergleichenden Anatomie des Brustschultergürtels', *Morphologisches Jahrbuch*, **64**, 1.
- GARSTANG, W. (1894, 1928). 'Preliminary note on a New Theory of the Phylogeny of the Chordata', *Zoologischer Anzeiger*, **17**, 122, & *Quarterly Journal of Microscopical Science*, **72**, 51.
- (1922). 'The Theory of Recapitulation. A Critical Restatement of the Biogenetic Law', *Journal of the Linnean Society of London, Zoology*, **35**, 81.
- (1928). 'The Origin and Evolution of Larval Forms', *Report of the British Association for the Advancement of Science, Section D*.
- GEGENBAUR, C. (1880). 'Kritische Bemerkungen über Polydactylie als Atavismus', *Morphologisches Jahrbuch*, **6**, 584.
- GEORGE, T. N. (1933). 'Palingenesis and Palaeontology', *Biological Reviews*, **8**, 125.
- GILFORD, H. (1911). *The Disorders of Postnatal Growth and Development*. London, 1911.

- GOLDSCHMIDT, R. (1923). 'Einige Materialien zur Theorie der abgestimmten Reaktionsgeschwindigkeiten', *Archiv für mikroskopische Anatomie und Entwicklungsmechanik*, **98**, 292.
- (1927). *Physiologische Theorie der Vererbung*. Berlin, 1927.
- (1934). 'Lymantria', *Bibliographia Genetica*, **11**, 4.
- GOODRICH, E. S. (1895). 'On the Coelom, Genital Ducts, and Nephridia', *Quarterly Journal of Microscopical Science*, **37**, 447.
- (1913). 'Metameric Segmentation and Homology', *Quarterly Journal of Microscopical Science*, **59**, 227.
- (1924). *Living Organisms*, p. 61. Oxford, 1924.
- (1930). *Studies on the Structure and Development of Vertebrates*, p. 612. London, 1930.
- GOODRICH, H. B., & HANSEN, I. B. (1931). 'The Postembryonic Development of Mendelian Characters in the Goldfish', *Journal of Experimental Zoology*, **59**, 337.
- HAECKEL, E. (1866). *Generelle Morphologie der Organismen*. II. 7 & 9. Berlin, 1866.
- (1875). *Ziele und Wege der heutigen Entwicklungsgeschichte*, p. 24. Jena, 1875.
- HAECKER, V. (1925). 'Aufgaben und Ergebnisse der Phänogenetik', *Bibliographia Genetica*, **1**, 95.
- HALDANE, J. B. S. (1932). 'The Time of Action of Genes and its Bearing on some Evolutionary Problems', *American Naturalist*, **66**, 5.
- (1932). *The Causes of Evolution*, p. 150. London, 1932.
- HALL, F. G. (1934). 'Haemoglobin Function in the Developing Chick', *Journal of Physiology*, **83**, 222.
- HARVEY, W. (1645). 'Exercitatio anatomica de motu cordis et sanguinis in animalibus' in *Adriani Spigelii Anatomica*, p. lxiii. Amsterdam, 1645.
- HERTWIG, O. (1906). 'Ueber die Stellung der vergleichenden Entwicklungslehre zur vergleichenden Anatomie, zur Systematik und Deszendenztheorie', *Handbuch der vergleichenden und experimentellen Entwicklungslehre der Wirbeltiere*, III. **3**, 149. Jena, 1906.
- (1916). *Das Werden der Organismen*, p. 216. Jena, 1916.
- HIS, W. (1874). *Unsere Körperform und das physiologische Problem ihrer Entstehung*. Leipzig, 1874.
- HOSKER, A. (1936). 'Studies on the epidermal structures of birds', *Philosophical Transactions of the Royal Society, B*, **226**, 143.
- HUNTER, J. (1861). *Essays and Observations*, **1**, 203. London.
- HURST, C. H. (1893). 'The Recapitulation Theory', *Natural Science*, **2**, 195.
- HUXLEY, J. S. (1923). 'Time Relations in Amphibian Metamorphosis', *Science Progress*, **17**, 606.
- (1924). 'Constant Differential Growth-Rates and their Significance', *Nature*, **114**, 895.
- (1932) *Problems of relative Growth*. London, 1932.
- HUXLEY, T. H. (1898). *Scientific Memoirs*, **1**, 303. London, 1898.
- HYATT, A. (1893). 'Phylogeny of an Acquired Characteristic', *American Naturalist*, **27**, 865.
- (1894). 'The Phylogeny of an Acquired Characteristic', *Proceedings of the American Philosophical Society*, **32**, 349.

- KAPPERS, C. U. A. (1928). *Three Lectures on Neurobiotaxis and other Subjects*. Copenhagen, 1928.
- KEIBEL, F. (1897). 'Das Biogenetische Grundgesetz und die Cenogenese', *Ergebnisse der Anatomie und Entwicklungsgeschichte*, **7**, 722.
- KIESLINGER, A. (1924). 'Neotenie, Persistenz, Degeneration', *Proceedings of the Academy of Sciences of Amsterdam*, **27**, 761.
- KLEINENBERG, N. (1886). 'Die Entstehung des Annelids aus der Larve von *Lopadorhynchus*', *Zeitschrift für wissenschaftliche Zoologie*, **44**, 212.
- KÖLLIKER, A. (1864). 'Über die Darwin'sche Schöpfungstheorie', *Zeitschrift für wissenschaftliche Zoologie*, **14**, 174.
- KOLLMANN, J. (1882). 'Das Ueberwintern von Frosch- und Tritonlarven und die Umwandlung des mexikanischen Axolotl', *Verhandlungen der naturforschenden Gesellschaft Basel*, **7**, 387.
- KRYŽANOWSKY, S. G. (1939). 'Das Rekapitulationsprinzip', *Acta Zoologica*, **20**, 1.
- KÜKENTHAL, W. (1897). 'Vergleichend-anatomische und entwicklungsgeschichtliche Untersuchungen an Sirenen.' *Semons Forschungsreisen* **4**, *Jenaische Denkschriften*, **7**, 74.
- LAMARCK, J. B. P. A. DE M. DE. (1873). *Philosophie zoologique*. (Édition C. Martins), **1**, 223. Paris, 1873.
- LANG, W. D. (1919). 'The Evolution of Ammonites', *Proceedings of the Geological Association*, **30**, 50.
- LANKESTER, E. R. (1894). 'Acquired Characters', *Nature*, **51**, 102.
- LEHMANN, F. E. (1938). 'Die morphologische Rekapitulation des Grundplans bei Wirbeltierembryonen', *Vierteljahrsschrift der naturforschenden Gesellschaft in Zürich. Beiblatt* **30**, 187. (*Festschrift Karl Hescheler*.)
- LILLIE, F. R. (1908). *The Development of the Chick*. New York, 1908.
- LOWE, P. R. (1928). 'Studies and Observations bearing on the Phylogeny of the Ostrich and its Allies', *Proceedings of the Zoological Society of London*, p. 185.
- (1933). 'On the Primitive Characters of the Penguins', *Proceedings of the Zoological Society of London*, 483.
- MACBRIDE, E. W. (1914). *Text-Book of Embryology*. I. *Invertebrata*, p. 650. London, 1914.
- MANGOLD, O. (1923). 'Transplantationsversuche zur Frage der Spezifität und der Bildung der Keimblätter', *Archiv für mikroskopische Anatomie und Entwicklungsmechanik*, **100**, 198.
- MATTHEW, W. D. (1927). 'The Evolution of the Mammals in the Eocene', *Proceedings of the Zoological Society of London*, p. 947.
- MECKEL, J. F. (1811). *Beiträge zur Vergleichenden Anatomie*. 2. *Entwurf einer Darstellung der zwischen dem Embryozustande der höheren Thiere und dem niederen Statt findenden Parallele*. Leipzig, 1811.
- MEHNERT, E. (1898). *Biomechanik*. Jena, 1898.
- METSCHNIKOFF, E. (1874). 'Embryologie der doppeltfüssigen Myriapoden', *Zeitschrift für wissenschaftliche Zoologie*, **24**, 253.
- MORGAN, T. H. (1916). *A Critique of the Theory of Evolution*. Princeton, 1916.
- (1924). 'Heredity of Embryonic Characters', *Scientific Monthly*, **18**, 5.
- (1926). *The Theory of the Gene*. Yale, 1926.

- MÜLLER, FRITZ. (1864). Für Darwin. Leipzig, 1864.
- MULLER, H. J. (1927). 'Artificial Transmutation of the Gene', *Science*, **66**, 84.
- NAEF, A. (1917). *Die individuelle Entwicklung organischer Formen als Urkunde ihrer Stammesgeschichte*. Jena, 1917.
- (1917). *Idealistische Morphologie und Phylogenetik*. Jena, 1919.
- NAUCK, E. T. (1931). 'Über umwegige Entwicklung', *Morphologisches Jahrbuch*, **66**, 65.
- NEEDHAM, J. (1930). 'The Biochemical Aspect of the Recapitulation Theory', *Biological Reviews*, **5**, 142.
- OSBORN, H. F. (1902). 'The Law of Adaptive Radiation', *American Naturalist*, **34**, p. 353.
- (1915). 'Origin of Single Character Differences', *American Naturalist*, **49**, 193.
- PAVLOV, A. P. (1901). 'Le Crétacé inférieur de la Russie et sa faune', *Nouveaux Mémoires de la Société impériale des Naturalistes de Moscou*, N.S. **16**, 87.
- RAW, F. (1927). 'Ontogenies of Trilobites and their Significance', *American Journal of Science*, **14**, 7, 131.
- REICHERT, C. B. (1838). *Vergleichende Entwicklungsgeschichte des Kopfes der nackten Amphibien*. Königsberg, 1838.
- RIDDLE, O. (1928). 'Internal Secretions in Evolution and Reproduction', *Scientific Monthly*, **26**, 216.
- ROBB, R. C. (1935-7). 'A Study of Mutations in Evolution', *Journal of Genetics*, **31**, 39, 47; **33**, 267; **34**, 477.
- RUBNER, M. (1908). *Das Problem der Lebensdauer und seine Beziehungen zu Wachstum und Ernährung*. München und Berlin, 1908.
- RUNNSTRÖM, J. and S. (1918-19). 'Über die Entwicklung von Cucumaria frondosa Gunnerus und Psolus phantopus Strassenfelt', *Bergens Museum Aarbok 1918-19. Naturvidenskabelig raekke*, **5**.
- RUNNSTRÖM, J. (1925). 'Zur experimentellen Analyse der Entwicklung von Antedon', *Archiv für Entwicklungsmechanik*, **105**, 63.
- RUSSELL, E. S. (1916). *Form and Function*. London, 1916.
- SCHINDEWOLF, O. H. (1936). *Paläontologie, Entwicklungslehre und Genetik*. Berlin, 1936.
- SCHULTZ, A. H. (1926). 'Fetal Growth of Man and other Primates', *Quarterly Review of Biology*, **1**, 465.
- SCHULZE, P. (1911). 'Über nachlaufende Entwicklung (Hysterotolie) einzelner Organe bei Schmetterlingen', *Archiv für Naturgeschichte*, **88**.
- SEDGWICK, A. (1894). 'On the Law of Development commonly known as von Baer's Law, and on the Significance of Ancestral Rudiments in Embryonic Development', *Quarterly Journal of Microscopical Science*, **36**, 35.
- (1909). 'The Influence of Darwin on the Study of Animal Embryology', *Darwin and Modern Science*, ed. A. C. Seward. Cambridge, 1909.
- SERRES, M. (1824). 'Recherches sur l'anatomie comparée des animaux invertébrés. 1. Que sont par rapport aux vertébrés et à l'homme les animaux invertébrés?' *Annales des Sciences Naturelles*, II, **2**, 248.

- SEWERTZOW, A. N. (1927). 'Über die Beziehungen zwischen der Ontogenese und der Phylogenese der Tiere', *Jenaische Zeitschrift für Naturwissenschaft*, **63**, 51.
- (1931). *Morphologische Gesetzmässigkeiten der Evolution*. Jena, 1931.
- SHUMWAY, W. (1932). 'The Recapitulation Theory', *Quarterly Review of Biology*, **7**, 93.
- SINNOTT, E. W., & DUNN, L. C. (1935). 'The effect of Genes on the Development of Size and Form', *Biological Reviews*, **10**, 123.
- SMITH, J. P. (1914). 'Acceleration of Development in Fossil Cephalopoda', *Leland Stanford Junior University Publications*, 1914.
- SMITH, P. E., & MACDOWELL, E. C. (1930). 'An Hereditary Anterior Pituitary Deficiency in the Mouse', *Anatomical Record*, **46**, 249.
- SMITH WOODWARD, A. (1923). *Presidential Address, Proceedings of the Linnean Society of London*, 135th Session, 1923, p. 30.
- SPATH, L. F. (1923). 'The Ammonoidea of the Gault', *Memoirs of the Palaeontographical Society*, p. 65.
- (1924). 'The Ammonites of the Blue Lias', *Proceedings of the Geological Association*, **35**, 186.
- (1925-6). 'Notes on Yorkshire Ammonites', *The Naturalist*, Sept. 1925, p. 268, and May 1926, pp. 137, 139.
- SPEMANN, H. (1938). *Embryonic Development and Induction*. New Haven, 1938.
- STEINER, H. (1918). 'Das Problem der Diastataxie des Vogelflügels', *Jenaische Zeitschrift für Naturwissenschaften*, **55**, 221.
- STOCKARD, C. R. (1910). 'The Influence of Alcohol and other Anaesthetics on Embryonic Development', *American Journal of Anatomy*, **10**, 369.
- (1930). 'The presence of a Factorial Basis for Characters lost in Evolution', *American Journal of Anatomy*, **45**, 345.
- STUBBLEFIELD, C. J. (1936). 'Cephalic Sutures and their Bearing on Current Classification of Trilobites', *Biological Reviews*, **11**, 407.
- SWINNERTON, H. H. (1937). 'Development and Evolution', *Report of the British Association for the Advancement of Science*, 1937, p. 57.
- TAN SIN HOK, (1932). 'On the genus Cycloclypeus', *Wetenschappliche Mededeelingen*, **19**, 3.
- THOMPSON, D'A. W. (1917). *On Growth and Form*, pp. 54, 549. Cambridge, 1917.
- THOMSON, A. (1924). 'Facial Development', *The Dental Record*, **44**, 119.
- TRUEMAN, A. E. (1922). 'The use of Gryphaea in the Correlation of the lower lias', *Geological Magazine*, **59**, 256.
- VERSLUYS, J. (1922). 'Über die Rückbildung der Kiemenbogen bei den Selachii', *Bijdragen tot de Dierkunde*, **22**, 95.
- WEDEKIND, R. (1920). 'Über Virenzperioden', *Sitzungsberichte der Gesellschaft für Beförderung der gesamten Naturwissenschaften zu Marburg*, 18.
- WEISMANN, A. (1904). *The Evolution Theory*, pp. 177, 186. (English translation.) London, 1904.
- WELLER, G. L. (1933). 'Development of the Thyroid, Parathyroid and Thymus Glands in Man', *Contributions to Embryology of the Carnegie Institution*, **24**, 93.

BIBLIOGRAPHY

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- WOLTERECK, R. (1905). 'Wurmkopf, Wurmtrumpf, und Trochophora',
Zoologischer Anzeiger, 28, 273.
- WOOD JONES, F. (1916). *Arboreal Man*. London, 1916.
- WÜRTEMBERGER, L. (1880). *Studien über die Stammesgeschichte der Ammoniten*.
Leipzig.

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